GOVERNMENT PUBLICATIONS
RECEIVED
JUL 21 1971
WILBUR CROSS LIBRARY
UNIVERSITY OF CONN.

TRANSPIRATION AND ITS CONTROL BY STOMATA IN A PINE FOREST

PAUL E. WAGGONER and NEIL C. TURNER

BULLETIN OF THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION, NEW HAVEN • No. 726, MAY 1971

Digitized by the Internet Archive
in 2011 with funding from
LYRASIS members and Sloan Foundation

http://www.archive.org/details/transpirationits00wagg

CONTENTS

	Summary	3
Chapter 1	Transpiration and Its Control—An Introduction	5
Chapter 2	A Description of Plantations, Weather, and Treatments	7
Chapter 3	The Foliage, Its Distribution and Effect on Shade	12
Chapter 4	The Stomata and Their Control	20
Chapter 5	Water Potential in the Foliage	31
Chapter 6	Bole Contraction, A Reflection of Water Potential	38
Chapter 7	Growth of the Boles, Internodes, and Needles	48
Chapter 8	The Soil Water	59
Chapter 9	Evaporation from the Forest	66
Chapter 10	Transpiration and Its Control—A Discussion	82
	Acknowledgments	84
	Literature Cited	85

Cover photo: A red pine canopy.

SUMMARY

The loss of water by a forest and the possible reduction of this loss by partial closure of the microscopic pores, or stomata, in the foliage were investigated for 5 years in two red pine plantations in eastern Connecticut.

The seasonal and diurnal variations in stomatal resistance were observed and related to light and shade. The water potential in the foliage changed in a daily cycle, and stomatal resistance was increased by dehydration. The boles or trunks of the trees shrank as the foliage dried each day, but the shrinkage lagged a few hours behind the cycle of radiation and foliage dehydration. Growth of the boles and elongation of the internodes and needles followed a normal pattern. The disappearance of soil water, mostly via evaporation, equaled insolation and also evaporation from an open pan of water.

Spraying with phenylmercuric acetate doubled stomatal resistance in all needles present during the springtime spray; later spraying scarcely affected the stomata in new needles. Bole growth was unaffected in the first year, but was decreased in subsequent years. After 3 years of spraying, the foliage was substantially decreased. Before any defoliation, however, the change in stomatal resistance promptly reduced the drying of foliage and shrinkage of the bole. Further, it retarded the loss of soil water significantly, and well within the quantity predicted from a comprehensive model of energy and water exchange within the forest. The removal of about a third of the foliage late in the experiment also decreased evaporation.

Thus a partial closure of the microscopic pores without destruction of vegetation altered the energy balance and conserved water in the soil. Over winter this yielded about 25 mm extra water to the groundwater that feeds the reservoirs.

TRANSPIRATION AND ITS CONTROL BY STOMATA IN A PINE FOREST

PAUL E. WAGGONER and NEIL C. TURNER

Chapter 1
TRANSPIRATION AND ITS CONTROL—AN INTRODUCTION

Connecticut's rainfall, 1200 mm in an average year, is modest, but adequate. Of this 1200 mm received by precipitation, only about half enters the lakes and streams, while the remaining half returns to the atmosphere as evaporation from the forests and farmland. A portion of this evaporates directly from the wet foliage, but the largest portion enters the soil and re-enters the atmosphere after passage through the plant. Thus in Connecticut, which has a million hectares of forests, a very large portion of the total rainfall in the state returns to the atmosphere from forests.

The droughts in the 1960's demonstrated the close balance between the supply and demand for water in the northeastern U.S.A. With an increase in both the population and the per capita use of water, the demand for water continues to grow. Indeed the water requirements are expected to be 25% above the present requirements within the next decade (U.S. Bureau of the Census, 1970). In the light of this, an understanding of water loss by vegetation is valuable, and means of controlling this loss need investigation.

This bulletin reports such a study. Since a substantial proportion of the evaporation occurs from forested land, experimental sites were established in two plantations of red pine in eastern Connecticut. We did not simply study the evaporation from a forest and the environmental and plant factors contributing to the loss, although this was indeed accomplished, but we also endeavored to manipulate the vegetation to reduce water loss, conserve groundwater, and ultimately increase the streamflow to the reservoirs.

The surface of the vegetation is perforated by many small pores, the stomata, through which the water extracted from the soil finally escapes into the atmosphere. Since the stomata are strategically located between the wet leaf interior and the dry atmosphere, they were a key part of our study. We observed the diurnal and seasonal pattern of their behavior and their response to light and dehydration of the foliage. Further, our attack on the control of water loss was at this junction between leaf and atmosphere.

Independently Ventura (1954) and Zelitch (1961) discovered that a number of biochemical compounds closed stomata without general

toxicity to foliage. Subsequently one of these compounds, phenylmercuric acetate (PMA), was shown to decrease transpiration relatively more than photosynthesis in leaves of tobacco (Zelitch and Waggoner, 1962), maize (Shimshi, 1963a), and cotton (Slatyer and Bierhuizen, 1964), and to decrease soil water loss more than growth in sunflower (Shimshi, 1963b) and a grass sward (Davenport, 1967). Moreover, preliminary studies revealed that PMA was effective in reducing the transpiration of isolated pine trees (Keller, 1966; Waggoner, 1967); therefore, we employed PMA in our study.

We must emphasize that our objective was not to demonstrate that PMA was a suitable chemical for treatment of watersheds in order to reduce water loss, but to demonstrate that closing stomata could indeed reduce evapotranspiration from a forest. Even though PMA was known to damage foliage at hot temperatures (Wadsworth, 1960), it was the logical choice at that time because its closure of stomata had been demonstrated. More recently a non-toxic plant hormone, abscisic acid, has been shown to close stomata (Mittelheuser and Van Steveninck, 1969; Jones and Mansfield, 1970) and, with more work, might today be our logical choice since it would not introduce a heavy metal into the environment.

Although manipulation of the stomata had been shown to reduce transpiration effectively in individual plants in pots, the effectiveness in a forest was very much in question. Thus using the data available in 1956, Penman (1956) concluded that meteorological parameters were of primary importance in determining the "potential" evaporation from vegetation, while plant factors had little effect. We accepted the predominance of weather in changing evaporation but attempted to reveal the smaller effects of vegetation upon actual evaporation by frequent observations in replicate adjacent plots. Our primary goal was to determine whether small increases in stomatal resistance would reduce the evaporation and measurably increase the water in the soil. However, as our treatments ultimately produced forest canopies differing by one third in leaf area, we also used this opportunity to study, in the final year, the effect of leaf area on evaporation.

Other attempts at increasing the water yield from a forested watershed have taken the drastic route of killing or removing the trees (Hewlett and Hibbert, 1961). Conversion of the mature forest to low vegetation increased the supply of water by 130 to 400 mm at Coweeta and by 100 to 300 mm at a number of other sites in the Northeast (Lull and Reinhart, 1967). Such drastic treatment, however, creates seasonal surges in streamflow and increases the risk of erosion. Stomatal closure does not suffer from these faults.

The following chapters describe in detail the observations and results from the 5-year study at Voluntown in eastern Connecticut. Two brief reports of some of our observations from the first 2 years of this study have already been published (Waggoner and Bravdo, 1967; Turner and Waggoner, 1968); we now report on the complete 5 years of observations.

Our primary concern was the conservation of soil water by reducing evaporation from the foliage. But we also sought to understand the mechanisms governing water loss by vegetation. Thus we observed the amount and distribution of foliage since it first absorbs and then employs the energy to evaporate water within the needles. We next examined the numerous stomatal pores, the variation in conductance as they were shaded, aged, or were sprayed with the PMA. Since the vapor loss changes the hydration, or water potential, within the foliage, we observed the diurnal change in the hydration within the canopy and the changes created by treatment with the stomata-closing PMA. Bole contraction is another measure of plant dehydration (Worrall, 1966) that we used for a more widespread measure of plant hydration. Finally, we measured the normal pattern of growth of the trees and studied whether treatment affected this pattern.

Soil water content was our most numerous observation. We employed this to follow the pattern of water depletion and replenishment throughout the season, and to determine the effect of shrunken stomata on these changes. From a knowledge of the rainfall we were able to use the soil water observations to calculate the evaporation from the forest and compare the untreated and treated foliage with theoretical changes in evaporation.

Chapter 2

A DESCRIPTION OF PLANTATIONS, WEATHER, AND TREATMENTS

The study of water loss and its control by phenylmercuric acetate (PMA) was conducted in two red pine (*Pinus resinosa* Ait.) plantations in the Pachaug State Forest at Voluntown, in eastern Connecticut. The forest, which comprises a mixture of hardwood and pine stands, is located on abandoned farmland. The first plantation, known to the foresters as the Daniels lot, was planted as seedlings at 2 m × 2 m intervals in an abandoned cornfield in 1931. For a decade it has yielded needles for the nearby Pachaug State Forest Nursery. The second plantation, known as the Bitgood lot, was established in 1944 by transplanting seedlings at approximately 2 m × 2 m intervals. The Daniels lot is 25 km and the Bitgood lot is 33 km north of Long Island Sound.

The soil at the first plantation is a Windsor loamy sand deposited in gentle slopes along the bank of the Myron Kinney Brook. The bulk or apparent density of the soil at 15 cm depth varied from 1.27 to 1.40 at ten sites, while at 30 cm it varied from 1.30 to 1.58.

On one day in 1965, 540 liters of water were applied to a square meter of the soil. Two days later, the soil beneath was examined to a depth of 3 meters, Table 1. The number of roots was observed by counting the number visible on 2700 cm^2 of soil profile. We found that the loamy fine sand of the top soil was underlain by a coarser stratum at about 1

Table 1. The roots and soil in the first plantation, 12 August 1965.

Depth, cm	Roots,[a] dm^{-2}	Water, %[d]	Bulk density	Silt, %[e]	Clay, %[e]	Texture[f]	AMHC[g]
15	15.0	20	1.32	16	2.6	lfs	10
30	4.0	18	1.30	16	1.2	lfs	10
60	3.8	11	1.48	8	2.3	fs	8
90	1.0	11	1.52	4	1.5	fs	8
120	0.5	16	1.67	11	0.8	fs	9
150	0.8	28	1.50	57	3.1	sil	21
180	Many[b]	32	1.55	68	2.7	sil	24
210	0.3	26	1.55	58	1.2	sil	22
240	....[c]	11	1.42	18	1.5	lvfs	11
270	....	9	1.37	42	0.8	vfsl	18
300	....	18	1.39	41	0.8	vfsl	17

[a] Roots dm^{-2} is number of roots visible on a soil profile between 0 and 15 cm depth or in 30 cm centered at 30, 60, . . ., 210 cm depth.
[b] Too numerous to count.
[c] No observations below 210 cm.
[d] v/v
[e] w/w
[f] U.S. Department of Agriculture (1951).
[g] Available moisture-holding capacity, per cent v/v calculated from texture (Hill, 1959).

meter. (This gravelly layer was later evident throughout the plantation as it plagued our driving of tubes for moisture measurement.) The gravelly layer, of course, held less water and had less available for roots. It had fewer roots than the soil above or below. Near 2 meters lay a silty stratum that held much water, had more available water, and grew an abundance of roots. A lens of silt laid down in a prehistoric ripple and 150 cm underground in 1965 had 75% silt and an available moisture-holding capacity of 25%; the entire zone, of course, had an average of only 57% silt.

The soil beneath 215 cm was sandier and had only 10 to 20% available moisture-holding capacity as calculated from its texture (Hill, 1959). Clearly the water poured upon the surface two days before had not reached this depth—and neither did the wide pit needed for counting roots reach 3 meters.

The soil of the second plantation, only 10 km northeast of the first, was also a Windsor loamy sand, but it was not examined in the same detail because its soil water content was not observed.

In 1966 the trees at the first plantation were about 15 meters in height and had a mean diameter of 18 cm at 140 cm from the ground (Fig 1A). In 1968 the stems had a mean cross sectional area of 48 m^2 per hectare or 209 square feet per acre. The plantation, which extended at least 30 meters beyond the area we used, was surrounded by hardwood forests.

Within the first plantation, 16 rectangular plots were laid out. The plots were 7 to 12 meters wide and 27 to 75 meters long. They encom-

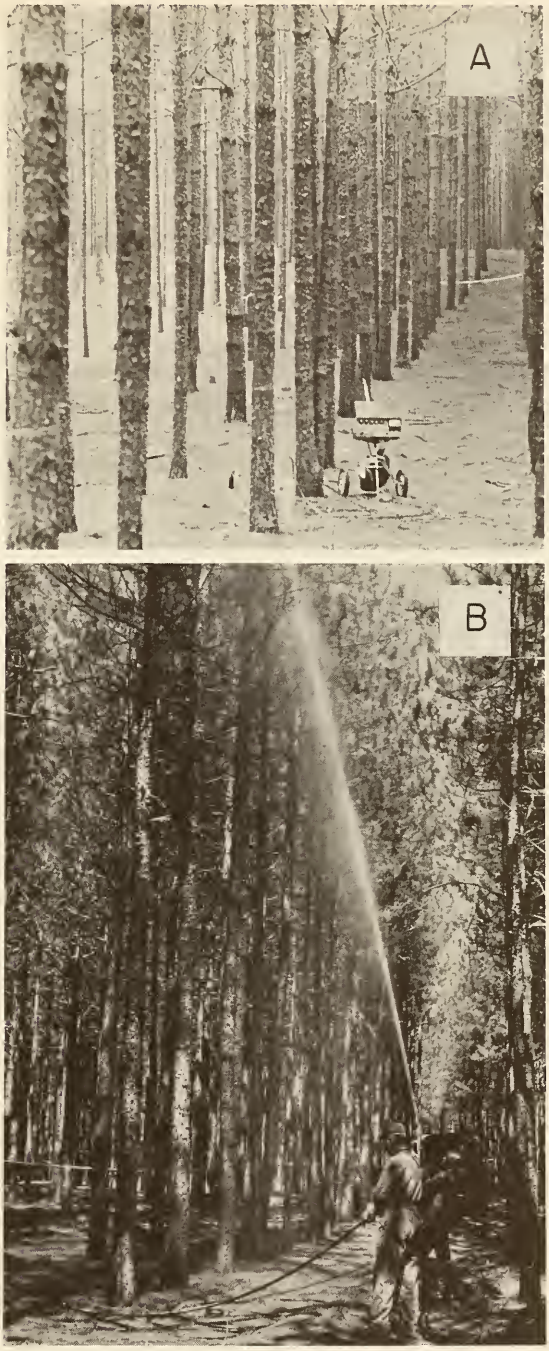

Fig. 1. A, View of first plantation in 1966; B, Spraying tree crowns with PMA.

passed about a thousand trees. The plots generally extended down a gradual slope and then a short distance up a somewhat steeper slope. No runoff was ever seen, however. In 1968 an infection by the brown root and butt rot (*Fomes annosus* [Fr.] Cke.) caused us to abandon four plots, and in the final two years, only 12 plots were used.

The trees at the second plantation had grown to about 11 meters tall by 1968. Well within the plantation, which was also surrounded by hardwood forest, 114 trees were selected in pairs. They had a mean diameter of 17 cm at 140 cm height.

The weather during the experiments is described by the monthly precipitation and the monthly evaporation from a U.S. Weather Bureau Class A pan. The precipitation (Table 2) was measured at the headquarters of the Pachaug State Forest which is near Voluntown, 5 km north of the first and 7 km southwest of the second plantation. The evaporation (Table 3) was measured at Coventry, Connecticut, and Kingston, Rhode Island, which are about 40 km northwest and 30 km southeast of the plantations. The observations are presented as averages of the two locations. We are grateful to the loyal observers who faithfully provided these climatic data.

From Tables 2 and 3 we see that during the months of June to September, in which the majority of our observations were concentrated, 1966 and 1969 had near normal amounts of precipitation and evaporation: high evaporation in July 1966 and low precipitation in June 1969 are two exceptions. The 1967 season was, however, wetter and duller than normal, whereas 1968 was noticeably drier and had greater than average evaporation during July and August.

The trees were sprayed once in 1966, thrice in 1967, and twice in 1968 with phenylmercuric acetate (PMA), which shrinks or narrows stomata. The PMA was obtained as 'Nildew AC30', a 30% solution manufactured

Table 2. Precipitation (mm) at Pachaug State Forest Headquarters.

Month	1966	1967	1968	1969	20-year Mean
1	71	33	86	36	92
2	86	64	28	56	89
3	61	157	168	86	108
4	30	91	46	114	102
5	119	150	91	91	87
6	86	66	109	28[a]	60
7	86	107	18	130	83
8	48	69	48	64	88
9	137	102	69	107	96
10	89	48	51	58	87
11	132	79	135	132	117
12	66	180	155	231	111

[a] Observations after May 1969 taken at Pachaug State Forest Nursery.

Table 3. Mean evaporation (mm) from a pan at Coventry, Connecticut, and Kingston, Rhode Island.

Month	1966	1967	1968	1969	13-year Mean
5	125	146	125	153[a]	136
6	136	150[a]	125	147	141
7	190	114	161	125	146
8	138	105	141	138	126
9	93	109	104	84	94
10	68	69[a]	71[a]	59[a]	71

[a] Evaporation at Kingston only.

by Naftone Inc., 425 Park Avenue, New York, N.Y. 10022. A 300 ppm or approximately thousandth molar solution of PMA was prepared; this is approximately the concentration that shrank stomata of tobacco (Zelitch and Waggoner, 1962) and other plants mentioned in Chapter 1. One of two wetting agents manufactured by Rohm and Haas, Philadelphia, was also mixed in the solution. In 1966 and 1967, 1000 ppm of Triton B-1956, a water insoluble nonionic modified phthalic glycerol alkyd resin, was used. But in 1968, 500 ppm of Triton X-100, a water soluble nonionic isooctyl phenoxy polyethoxy ethoxylate, was used in place of the Triton B-1956. Since Triton X-100 is water soluble, it produced a solution of PMA rather than the dispersion produced by Triton B-1956.

The solution was applied from the ground by a hydraulic sprayer jet that could strike one crown at a time (Fig. 1B). The wetting of the uppermost foliage was verified by examining shoots pruned from the crowns. In 1966 after one spray, analysis of foliage by L. G. Keirstead of the Station's Analytical Chemistry Department showed 4 to 19 ppm of mercury in the treated and 0.1 or less ppm in the adjacent untreated foliage.

The first plantation was sprayed on 2 June 1966; 8 June and 19 July 1967; and 4 June and 15 July 1968. It was also sprayed on 1 June 1967, but that Nildew was a year old, the behavior of the pine stomata and bioassay with tobacco leaf discs (Zelitch, 1961) indicated that the Nildew had deteriorated, and the pines may be considered as having received only two effective sprays in 1967. The second plantation was sprayed only on 4 June and 15 July 1968.

The plots of trees sprayed were selected as follows. The 16 plots in the first plantation were divided into eight pairs or replicates. One of each pair was selected for treatment by the flip of a coin. The area sprayed was 0.4 hectare, it encompassed 570 trees, and at each spray it received 3500 to 4000 liters of solution in 1966 and 1967 and 2800 to 3200 liters in 1968.

In the second plantation and on the first occasion in 1968, a randomly-selected individual tree of each of 45 pairs was treated. On the second occasion, 22 of those untreated and 23 of those treated on the first oc-

casion were sprayed. In addition, one of each of ten new pairs was sprayed. On the second occasion, four more trees were sprayed with wetting agent *alone;* subsequently these behaved and appeared the same as untreated trees and were considered to be untreated. Consequently, the number of trees was:

Untreated	— 37
First treatment	— 23
Second treatment	— 32
Both treatments	— 22
Total	— 114

Since damage of the foliage had been observed in greenhouse studies (Waggoner, 1967), we carefully checked the foliage after each spraying. It was not affected at either plantation except when sprayed on 4 June, 1968 with the PMA and Triton X-100. A few sprayed needles at both plantations became chlorotic and fell.

We now go on in Chapter 3 to describe the trees further by showing the leaf area, defoliation, and absorption of illumination in the first plantation.

Chapter 3

THE FOLIAGE, ITS DISTRIBUTION AND EFFECT ON SHADE

First, foliage on a tree was weighed. A tree with a diameter similar to the plantation mean was found, needles were stripped from the tree, and the needles were weighed according to their year of development. The total dry weight of foliage of 9 kg corresponds to a foliage weight of 16,750 kg ha^{-1} at the observed density of 1880 trees per ha.

The sample tree had 17 live whorls. A few of the needles that had emerged 5 years earlier were still present on the lower seven whorls, but the bulk of the foliage was less than 5 years old in the lower canopy and less than 4 years old in the fourth to tenth whorls. The sample tree had 28,000 or 2.4 kg of 1-year-old fascicles, 45,000 or 3.4 kg of 2-year-old, and 35,000 or 3.1 kg of older fascicles.

Next, a broader sample of foliage was obtained by trapping fallen needles. This both verified the quantity of foliage on the untreated forest and revealed whether our treatment with PMA altered the quantity. In the first plantation we placed buckets or traps, 19.0 cm in diameter, on the ground south and 60 cm from the base of six trees within each of the eight treated and eight untreated plots. In the second plantation traps were placed beneath 114 trees. In June 1968 the 96 trees at the first plantation were reduced to 72 as the four infected plots were abandoned (Chapter 2). The traps were placed in the first plantation on 15 September 1967 and in the second plantation on 4 June 1968. The number of needles caught in the traps was observed peri-

odically throughout the year. The traps were emptied after each observation. To analyze the foliage caught in the 19 cm diameter traps we simply calculated the mean and standard error of the number of fascicles (i.e. pairs of needles) collected between two observations. This simplification avoided complications caused by missing observations and variable numbers of replicates, and the standard errors were still sufficiently small to reveal differences between treatments.

The normal pattern of needle fall in red pine plantations is seen in the first and third columns of Table 4 and by the accumulation of the same numbers of fallen needles in Fig. 2. A few needles fall between April and mid-September, but most fall between mid-September and late November. A few fall during the winter.

The validity of the 19-cm-diameter traps as samplers can be tested by comparing the amount that they caught with the annual growth of needles measured on Connecticut red pine by G. R. Stephens (unpublished). In the first plantation the catch was 137 fascicles in 1968-1969 and 127 in 1969-1970. Since these fascicles weighed 63 mg each, the annual catches were 3000 and 2800 kg ha^{-1}. In the second plantation, the catches were 174 and 146 in the two years. Since these also weighed about 63 mg each, the annual catches were 3800 and 3200 kg ha^{-1}. All

Table 4. Number of fascicles caught by the 285 cm^2 traps during periods ending on dates tabulated. A single observation of dry weight in mg is shown in parentheses on 9 July 1968. The traps were placed on 15 September 1967 at the first plantation and 4 June 1968 at the second plantation, and emptied after each observation.

Date	First Plantation		Second Plantation			
	Treatment		Treatment			
	Untreated	Treated	None	First	Second	Both
1967						
Oct. 25	66.0±2.0	112.0±4.0	.....	.....	.....	.....
Dec. 7	16.0±1.0	16.0±1.0	.....	.....	.....	.....
1968						
May 7	16.0±1.0	16.0±1.0	.....	.....	.....	.....
June 3	3.3±0.3	2.7±0.3	.....	.....	.....	.....
July 9	4.5±0.5	9.4±0.8	5.8±0.6	14.0±1.0	5.4±0.6	15.0±1.0
(July 9	282±31	633±28	369±33	958±110	321±29	978±94)
Aug. 8	3.0±0.5	7.6±0.8	3.9±0.3	8.8±0.6	4.7±0.3	8.6±0.6
Sept. 9	4.6±0.8	12.0±0.7	5.2±0.5	16.0±1.0	6.3±0.6	19.0±1.0
Oct. 18	58.0±2.0	101.0±4.0	44.0±2.0	74.0±4.0	46.0±3.0	69.0±4.0
Nov. 25	44.0±2.0	45.0±2.0	65.0±3.0	80.0±4.0	71.0±4.0	78.0±4.0
1969						
April 17	23.0±1.0	18.0±1.0	50.0±3.0	67.0±3.0	54.0±4.0	56.0±3.0
July 11	7.3±0.5	3.9±0.3	6.7±0.4	7.6±0.6	8.0±0.6	7.7±0.7
Sept. 24	15.0±1.0	10.0±1.0	13.0±1.0	13.0±1.0	12.0±1.0	12.0±1.0
Nov. 19	79.0±3.0	55.0±1.0	70.0±3.0	66.0±4.0	62.0±3.0	69.0±4.0
1970						
April 28	26.0±1.0	19.0±1.0	56.0±3.0	54.0±3.0	61.0±4.0	50.0±3.0

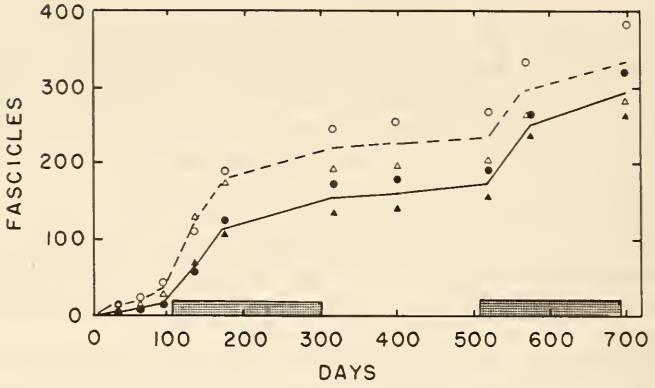

Fig. 2. Fascicles accumulated in traps beneath untreated trees (——) in the first (▲) and second (●) plantations, and beneath twice treated trees (----) in the first (△) and second (○) plantations. Days accumulated from 4 June 1968. Shading identifies autumn and winter.

four catches were well within the range of 2000 to 6000 kg ha^{-1} annual growth of needles that Stephens weighed on other Connecticut red pine. Further, the greater amount of foliage in the second plantation, which was evident to the eye, is confirmed by the catch of fallen needles.

The effect of the PMA treatment can now be examined. In both plantations the spray approximately doubled the fall of needles between spraying in June 1968 and mid-October 1968. The results in the second plantation show the first spray caused the defoliation. On the other hand, the fall between October 1968 and November 1968, i.e. with no further spraying, was little if any greater beneath sprayed than unsprayed trees. Considering one whole year, which we take as 4 June 1968 to 11 July 1969, we see the normal fall of 140 to 180 fascicles is increased to 200 to 270 by spraying. This increase is a third to a half of the normal fall. Presumably if this increase were continued for three years, as during 1966-68 in the first plantation, the standing crop of foliage would be decreased a third to a half.

On six occasions during 1967-68 the average weight of the fascicles caught in the traps under the PMA treated trees was 63.4 mg, while that of the unsprayed fascicles was 63.2 mg. This equality of weight suggests that the foliage that fell into the traps was from all whorls of the treated trees and not simply from the lower or upper portions of the crown.

To establish the source of the needles caught in the traps more directly, 10 trees from the first plantation, and 16 trees from the second plantation were sampled on four occasions between June 1968 and November 1969. On each occasion a single branch from the fourth to sixth whorls from the top of each tree was removed, and the fascicles removed and counted by year of origin. On each date a branch from the same whorl was sampled. On the first sampling date, the bulk of the foliage was

Table 5. Number of fascicles per cm of internode (± standard error) on branches from the fourth to sixth whorls from treated and untreated trees. The trees were sampled in the four months as noted at A, B, C and D, and fascicles were tallied according to year of origin.

Year of Origin	First plantation		Second plantation			
	Treatment		Treatment			
	Untreated	Treated	None	First	Second	Both
			A. June 1968			
1967	10.0±0.6	10.6±0.2	10.0±0.4	*	*	*
1966	11.3±0.4	9.8±1.0	11.1±0.4	*	*	*
1965	7.6±0.6	1.9±1.0	5.8±1.0	*	*	*
1964	1.2±0.1	0	0.4±0.2	*	*	*
			B. September 1968			
1968	12.2±0.3	11.4±0.7	9.5±0.6	9.6±0.4	8.5±0.1	8.9±0.8
1967	10.3±0.5	9.7±0.6	10.6±0.9	8.9±0.6	10.1±0.4	7.8±1.0
1966	10.5±0.5	8.3±1.0	9.9±1.0	5.0±2.0	9.3±1.0	4.4±1.0
1965	5.9±0.4	0.4±0.3	4.1±1.0	0.4±0.5	3.7±2.0	0.1±0.1
1964	0.7±0.5	0	0	0	0	0
			C. November 1968			
1968	11.5±1.0	10.6±1.0	9.9±0.9	9.6±0.5	8.8±0.5	9.3±0.6
1967	10.0±0.5	7.8±0.8	9.7±0.6	6.0±4.0	8.8±0.8	8.1±0.9
1966	9.6±2.0	0.2±0.1	4.6±2.0	3.6±4.0	4.7±4.0	1.1±0.4
1965	2.6±1.0	0	0.3±0.4	0	0.2±0.3	0.2±0.2
1964	0	0	0	0	0	0
			D. November 1969			
1969	10.4±0.5	11.2±1.0	8.8±0.5	9.3±2.0	9.9±1.0	7.3±2.0
1968	11.7±0.4	10.5±2.0	9.1±0.9	9.4±1.0	8.5±0.8	10.0±0.8
1967	6.1±1.0	1.8±0.7	5.2±2.0	5.0±2.0	5.6±1.0	6.1±3.0
1966	0.4±0.3	0	0.3±0.3	0	0.6±0.5	0
1965	0	0	0	0	0	0

* Spray treatment not yet applied.

3 years old or less, with a few 4-year-old needles still attached (first and third columns, Table 5); this is consistent with our earlier findings from the sampled tree. Table 5 shows that the 3-year-old fascicles were fewer per cm than were the 1- and 2-year-old fascicles, and it was the 3- and 4-year-old fascicles that were shed during September and October. Surprisingly, the number of fascicles per cm of internode was similar in both plantations even though as noted earlier, the foliage appeared more luxurious at the second plantation. As we shall show later, this was largely the result of longer internodes, not longer or denser fascicles.

The additional needles caught in the traps under the trees treated with PMA were clearly the older needles (Table 5). Prior to treatment in 1968, the treated trees at the first plantation had shed almost an extra year's needles. Treatment in 1968 increased the loss so that by

Fig. 3. Four-year-old branches from the first plantation sampled on 7 May 1969. The left branch was from a treated tree and the right branch from an untreated tree. The numbers indicate the age in years of the internodes.

November 1968, after the needle fall for that year, more than an extra year's needles had been shed. This is clearly seen in the sampled branches shown in Fig. 3. When the treatment with PMA was omitted for one year, the needle fall was smaller in the treated plots (Table 4), but the foliage did not completely recover to that in the untreated trees (Table 5, November 1969).

At the second plantation, the foliage sprayed on 4 June 1968 had fewer older needles by September 9. After the needle fall in 1968 there were slightly fewer needles on the trees treated on 4 June. By contrast, the second spray had no effect, and by November 1969 there were no differences in numbers of fascicles per cm of internode between treated and untreated trees, whatever the date of treatment. Apparently the

effect of treatment with PMA was progressively more damaging, but the foliage quickly recovered in density once treatment was terminated.

Plant pathologists, who use phenyl mercurial compounds to eradicate fungal infection in foliage, are familiar with its yellowing of foliage in warm weather (Wadsworth, 1960). Because of the noticeable discoloration of foliage by the first spray in 1968, the damage to the needles was evaluated before and after the period of maximum needle fall in 1968 (Table 6). The percentage of the needle length of 25 fascicles that was not green was observed. The yellowing or browning of the needles increased with age. Treatment with PMA increased yellowing of the older needles by September; these were the needles subsequently shed, so that by November, after the major needle fall, the yellowing of the remaining needles was not statistically different from the controls.

Shade or illumination beneath the crown of the trees should provide a further indication of how much foliage the trees bore and how much was removed by the sprays. The difference between illumination in a clearing and on the forest floor should roughly indicate the foliage area. This indication is only approximate because the absorption coefficient for light is not exactly known and because wood as well as needles absorbs light. On the other hand, the absorption coefficients of wood of treated and untreated trees should be essentially the same, and the difference between illumination beneath the two sorts of trees should more precisely indicate any defoliation. Hence in the first plantation and beneath overcast skies at 1100, 1200 and 1300 hours E.S.T. on 9 September 1968, and about 1000 on 21 June and 12 July 1969, illumination was measured beneath 72 trees by a foot-candle meter (Weston Instrument Co., 614 Frelinghuysen Avenue, Newark, New Jersey 07114).

Table 6. Percentage (± standard error) of needle length that was not green. Samples of 25 fascicles were taken from fourth to sixth whorls and from four or five years of origin.

Year of Origin	First plantation		Second plantation			
	Treatment		Treatment			
	Untreated	Treated	None	First	Second	Both
			A. September 1968			
1968	0	0	0.8±0.6	17.6±20.0	1.6±2.0	0.1± 0.1
1967	2.9±1.0	2.8± 1.0	3.4±1.0	4.7± 4.0	3.4±4.0	15.4±13.0
1966	6.5±2.0	10.6± 3.0	5.2±2.0	15.9± 8.0	7.7±3.0	13.8± 4.0
1965	7.1±2.0	40.4±15.0	10.8±7.0	.....	5.4±2.0	63.2± 6.0
1964	10.5±5.0	.....	.....	.....	.....	.....
			B. November 1968			
1968	0.6±0.4	0.9± 0.4	1.7±0.5	1.4± 0.8	1.4±0.6	1.7± 1.0
1967	2.5±0.5	2.6± 0.9	4.0±0.9	6.1± 2.0	4.6±4.0	10.2± 7.0
1966	4.0±2.0	6.2± 4.0	1.8±0.4	3.0± 3.0	4.1±2.0	7.6± 6.0
1965	6.2±4.0	.....	.....	.....	.....	.....

These were the same trees whose needles were trapped. Treated and untreated trees were observed alternately, occasional observations were made in clearings, and an entire set of observations required 30 to 45 minutes.

On the first day, illumination beneath the untreated trees was 30 to 40% of that in a clearing. On the last day it was about the same. The absorption of illumination in a canopy has often been represented by Beer's Law:

$$-\log_e (I_b/I_a) = kF_u \qquad (1)$$

where I is the illumination above (a) and below (b) untreated foliage of projected area F_u with an extinction coefficient k. The observed 30 to 40% transmission corresponds to a logarithm of −1, making the estimate of F_u equal to 1/k. The range of k, albeit in flat foliage, is 0.3 to 1.0 (Saeki, 1963), making the estimate of projected leaf area (F_u) equal to 1 to 3. This was indeed the range of areas observed by G. R. Stephens (unpublished) in several Connecticut plantations of red pine.

This estimate of the projected area can be compared with the area calculated from the weight of foliage on the tree. The annual catch of needles, in 72 traps and two years, was 2900 kg ha^{-1} in untreated trees. Table 5 shows that these trees held 3 to 4 years of needles. Therefore, multiplying 2900 kg ha^{-1} by 3½, we estimated that the trees had 10,000 kg ha^{-1} of foliage. This is less than the 16,750 kg ha^{-1} of foliage upon the sampled median-diameter tree, but since it is based on a much greater number of observations, we preferred it in calculating the projected leaf area.

The projected foliage area was calculated from the 10,000 kg ha^{-1} weight of foliage by multiplying by the mean of the two fascicle widths (0.12 and 0.15 cm), the length (12 cm) and dividing by the 63 mg per fascicle. This gave an area of 2.6 ha ha^{-1}; the range of areas established by the absorption of illumination, therefore, compared favorably with this estimate.

Since we shall later need an estimate of foliar surface area, it is now calculated. Red pine needles are produced in pairs from a bundle sheath; a pair of needles constitutes a fascicle. Each needle has one flat surface which faces the flat surface of the other needle in the fascicle. A cross section through a needle is similar to a cross section through half an ellipse. To calculate the surface area (A) of a red pine fascicle in cm^2, each fascicle can be treated as two halves of an elliptical cylinder:

$$A = L\left[\left(\sqrt{\frac{\pi}{2}}\sqrt{D^2 + W^2}\right) + 2W\right] \qquad (2)$$

where L is the length of the needle, W is the lesser fascicle diameter measured at ½ L, and D is the greater fascicle diameter when the two needles are placed together and measured at ½ L. Treating the fascicle as a cylindrical ellipse, rather than a tapering cylindrical ellipse, over-

estimates the true surface area by less than 6%. The average surface area of 150 fascicles was 7.8 cm^2. This corresponds to a foliar surface of 12.4 cm^2 of epidermis per cm^2 of land, well within the range of 5 to 17 in other *Pinus* spp. (Tadaki, 1966).

Having established the projected and total surface area of the untreated forest, we return to our observations of illumination. The comparison of treated and untreated trees is summarized in Table 7. It is clear from the mean values of illumination beneath treated and untreated trees presented in the upper two lines that more light was transmitted by the treated trees.

If we write Beer's Law for I_t and F_t, the illumination beneath and foliar area of treated canopies, and then subtract this second expression from the one for untreated foliage, we obtain:

$$\log_e (I_t/I_u) = k (F_u - F_t) = k F_u (F_u - F_t) / F_u \qquad (3)$$

The mean differences in the logarithm of illumination between each part of treated and untreated trees are given in the third line of Table 7. These differences were much greater than their standard errors, establishing the statistical significance of the difference in defoliation and transmission of illumination caused by the spray. The differences were about 0.2 in logarithmic units, which indicates that about a fifth more light was transmitted through sprayed than unsprayed foliage. This observation must be reconciled with earlier data. Observations of the foliage itself, which have already been presented, indicate that by late 1968 a half to one third of the foliage in the first plantation had been removed by spraying, i.e.

$$0.3 < (F_u - F_t)/F_u < 0.5$$

Furthermore, the shade beneath the untreated trees has already been shown to correspond to:

$$kF_u = 1.0$$

This kF_u includes, of course, the shade of the branches and would have to be changed to, say, 0.6 for foliage alone. The product of 0.3 to 0.5

Table 7. Mean illumination (I) in foot-candles beneath untreated (u) and treated (t) trees near midday in cloudy weather, and the mean logarithm of their ratio.

	Date				
	1968			1969	
	September 9			June 21	July 12
	1200h	1300h	1400h	1100h	1000h
Untreated	370	182	181	764	338
Treated	473	242	220	959	408
$\log_e \frac{I_t}{I_u}$	.24±.04	.28±.06	.19±.04	.22±.03	.19±.04

defoliation and the 0.6 for kF_u then makes $\log_e (I_t/I_u)$ equal to 0.2, which is consistent with the mean observed in Table 7.

Having established the weight and distribution of foliage on the trees and estimated the foliage area by several means, in the next chapter we turn to the porosity of the foliage, which controls how much water will be evaporated per unit area of foliage.

Chapter 4

THE STOMATA AND THEIR CONTROL

Since the cuticle of foliage is only slightly permeable to water, transpiration is controlled—or so it logically seems—by the frequency and varying dimensions of the microscopic pores or stomata that connect the moist interior of a needle or leaf to the arid atmosphere outside. The stomatal conductance or its reciprocal, stomatal resistance, is therefore a fundamentally important characteristic in the hydrology of the forest. The resistance has a further importance in our investigations because the treatment with PMA was designed to alter the evaporation or hydrology by altering stomatal resistance.

The discussion of stomata proceeds in the following steps. First, the needles and the arrangement of pores are described. Next the peculiar wax in them is measured. Our method of measuring stomatal resistance is described. Then the normal diurnal, height, and seasonal courses of stomatal resistance are shown. As these courses are examined, the effects of light, dehydration, and PMA upon stomatal resistance are revealed.

The stomata occur in rows along the needle on both the flat and convex surfaces (Fig. 4A); they number approximately 5000 per cm^2. The two guard cells surrounding the stomatal pore are found at the bottom of a pit approximately 20 microns deep. The pits are filled with wax which is readily stained with Sudan IV (Fig. 4B). The wax cannot be observed in the youngest stomatal pits deep within the protective bundle sheath at the base of the needle, but each pit is filled with wax when it emerges from the sheath. It is, therefore, probably loosely packed flakes of cuticular wax, which enter the stomatal cavity as the needle emerges from the bundle sheath.

When needles were dipped in chloroform for 30 seconds, 0.01 g of wax was removed per g (dry wt) of needle or 7×10^{-5} g of wax per cm^2 of needle; this includes cuticular wax and that within the stomatal cavity. The quantity of wax recovered by this standard procedure did not vary during the growing season or with the age of the needles. Since we shall see that stomatal resistance varies from day to night, we assume that the wax in the stomata does not greatly alter stomatal control of transpiration.

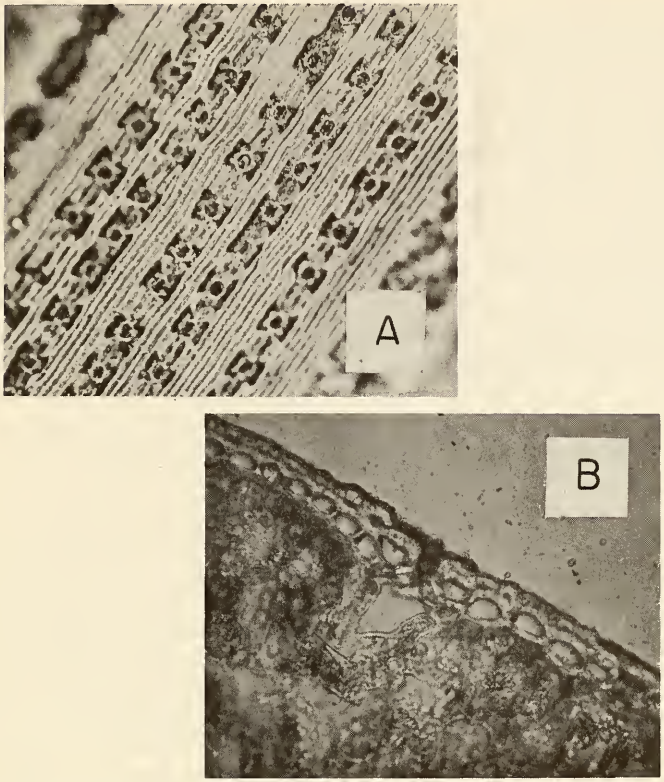

Fig. 4. A, View of the surface of a red pine needle, showing the rows of stomata; B, Cross section of a pine stomata stained with Sudan IV.

The presence of wax in the stomatal cavity prevents measurement of stomatal aperture directly under the microscope. Furthermore, the presence of the wax and the depth of the cavity precludes the use of silicone rubber impressions (Sampson, 1961; Zelitch, 1961). These limitations have led to the development of infiltration methods and porometer methods for measuring stomatal aperture in conifers. The degree of infiltration by a solvent or dye at atmospheric pressure can be used as a measure of stomatal aperture (Oppenheimer and Engelberg, 1965). Fry and Walker (1967) described a pressure infiltration method, which is more sensitive. The development of the diffusion porometer for the measurement of relative stomatal aperture in broad leaves (Wallihan, 1964) was followed by its modification for both broad leaves and pine needles (Kramer, 1969; Turner *et al.*, 1969).

In 1966 we estimated stomatal apertures by Oppenheimer and Engelberg's infiltration technique. Immediately after cutting, sunlit needles were dipped into a solution containing 8 g of crystal violet dissolved in 20 ml of ethanol to which 90 ml of ether and 90 ml of chloroform had

been added. After 2 to 5 minutes the needles were washed in secondary butanol and the differences between trees estimated by ranking the needles from the most to the least infiltrated.

In the years following 1966, we estimated the stomatal aperture with a ventilated diffusion porometer (Turner *et al.*, 1969; Turner and Parlange, 1970). The porometer has two basic parts: an acrylic chamber into which pine needles can be inserted (Fig. 5) and a meter to show the changes in humidity within the chamber. With a bunch of five fascicles inserted 4 cm into the chamber, the time for a fixed change in humidity was observed. The observed times can be used as a measure of relative stomatal aperture or converted into absolute values of the epidermal resistance to diffusion of water vapor. Turner and Parlange (1970) have shown that the stomatal resistance to diffusion (r_s) can be accurately calculated from the observed times (t):

$$r_s = \left\{ At \Big/ \left[\log_e \frac{(C_\infty - C_o)}{(C_\infty - C_t)} \right] \left[V_s + V_c \right] \right\} - r_p \qquad (4)$$

where A is the surface area of the needles within the chamber of volume V_c. V_s is the effective volume of the sensor, i.e. the capacity of the sensor to absorb water; and C_∞, C_o and C_t are the relative humidities within the chamber when saturated ($C_\infty = 100$), at $t = 0$, and at time t, respectively. C_o and C_t are given by the manufacturer (Hygrodynamics, Inc., 949 Selim Road, Silver Spring, Md., U.S.A. 20910) of the lithium chloride humidity sensor for different temperatures and electrical resistances of the sensor. The porometer resistance r_p, which is largely governed by the boundary layer resistance, was obtained from dead needles dipped in water containing a small quantity of wetting agent. Both V_s and r_p are temperature dependent as given in Table 8. V_c was 32 cm^3. A, calculated from Equation 2 and corrected for the 6% decrease due to the taper of the needles, was 12.4 ± 0.2 cm^2.

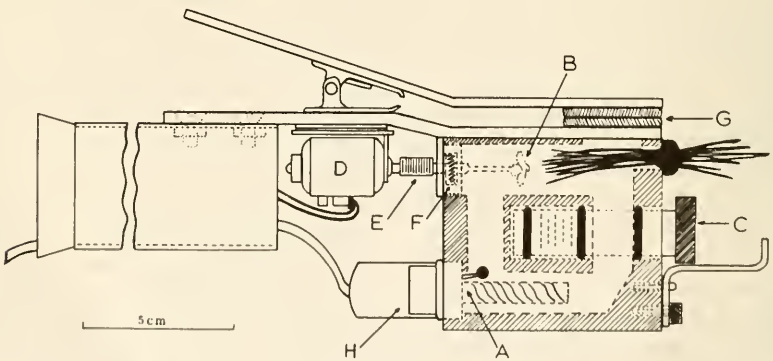

Fig. 5. Side view of ventilated diffusion porometer for use with pine needles. A, humidity sensor and bead thermistor; B, fan; C, plunger containing desiccant; D, motor; E, rubber coupling; F, sealed bearing; G, closed-cell sponge rubber; H, electrical connector.

Table 8. Effect of temperature on the effective sensor capacity (V_s) and the porometer resistance (r_p) for pine needles.

Temperature	15C	20C	25C	30C	35C
V_s	137	110	83	56	29
r_p	1.72	1.66	1.62	1.57	1.52

Sampling for the determination of stomatal resistance occurred at intervals throughout the season. In 1966 infiltration resistances were observed on four occasions, 23 June, 7 July, 26 August and 9 September. In 1967 stomatal resistances were measured with the porometer approximately every two weeks from 1 June until 25 October, whereas only occasional observations were made in 1968 and 1969.

For an individual tree the calculated stomatal resistances are means of at least duplicate samples on needles of the same year. Where needles of more than one year were sampled from the same branch, samples were taken within 5 minutes of removal of the branch from the tree; a change in stomatal resistance was not observed within this period. To establish the seasonal trends and treatment effects on stomatal resistance an average of eight (minimum of three) trees in each treatment were sampled on any one occasion. Only branches from the fourth to sixth whorls from the tree-top were sampled. On a number of days in 1967 the diurnal variation in resistance was observed in both upper (fourth to sixth) and lower (below the tenth) whorls from a pair of trees, one sprayed with PMA and one unsprayed.

Immediately prior to sampling, the radiation above the branch to be sampled was measured with an omnidirectional meter constructed from 2 silicon photovoltaic cells placed back-to-back inside a table-tennis ball that acted as a diffuser. This was placed near the cutter of the pole pruner used to sample the foliage. The meter was calibrated with an Eppley pyrheliometer. Radiation measurements were obtained only in 1967.

The diurnal change in stomatal resistance from just before sunrise to 3 hours after sunset was observed during the three 24-hour periods between 28 June and 27 July 1967 (Fig. 6). The stomata opened quickly as the sun rose in the morning, and the resistance declined to a minimum of 15 to 20 sec cm^{-1} in the upper branches at midday. Resistances increased again after sunset when the stomata closed. In the lower branches, i.e. those below the tenth whorl, the resistances were more variable, were generally higher than in the better lit upper branches, and reached a minimum resistance of approximately 24 to 27 sec cm^{-1} at midday (Fig. 6).

The new foliage which emerged in July gave us an opportunity to compare the diurnal change in stomatal resistance of newly-emerged needles and those one year older. Fig. 7 shows that between 0800 and

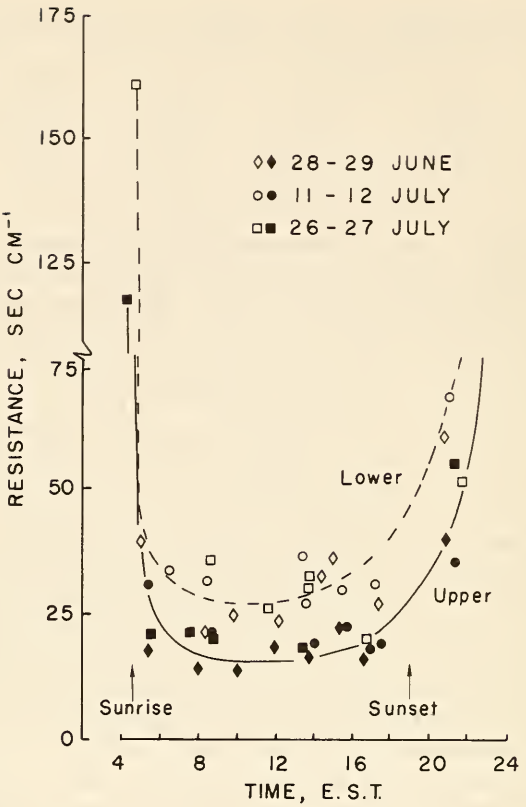

Fig. 6. Diurnal variation in stomatal resistance of foliage from the upper six whorls (closed symbols), or whorls below the tenth (open symbols) on three dates in 1967.

1800 hours E.S.T. the resistance in the newly-emerged needles was approximately half that of needles a year older; the newly-emerged needles had resistances of 7 to 12 sec cm^{-1}, whereas in the 1-year-old needles the resistances were between 18 and 24 cm sec^{-1}.

The effects of PMA on the diurnal change in stomatal resistance are shown in Fig. 8. The year-old fascicles had received one spray of PMA 8 weeks before and a second spray 1 week before these observations of stomatal resistance. The newly-emerged fascicles had not emerged at the time of the first spray and therefore had received only the PMA applied 1 week earlier. Both treated and untreated needles closed their stomata at night; but during the day, the treated year-old needles had resistances approximately twice as great as the untreated needles: between 0800 and 1800 hours E.S.T. the resistances ranged between 30 and 60 sec cm^{-1} in the treated needles, whereas the resistances were

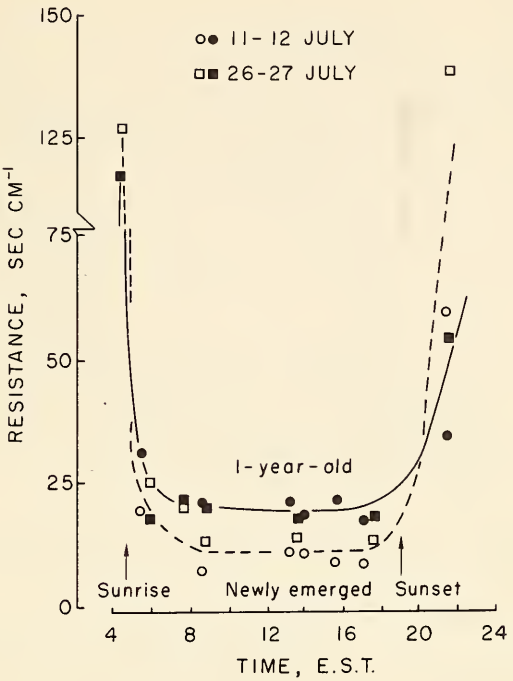

Fig. 7. Diurnal variation in stomatal resistance of newly-emerged (open symbols) and 1-year-old (closed symbols) fascicles on two dates in 1967.

between 20 and 25 sec cm^{-1} in the untreated ones (Fig. 8A). On the other hand, the newly-emerged needles were unaffected by the PMA (Fig. 8B).

Light is a primary determinant of stomatal aperture (Loftfield, 1921), and its effect can be seen in the diurnal change. We can construct the daily march of radiation from our observations of omnidirectional radiation above the sampled foliage on 28 to 29 June, 11 to 12 July and 26 to 27 July (Fig. 9). In the upper six whorls the radiation increased slowly at first, then more rapidly as the sun climbed and sunlight penetrated into the stand, and reached a maximum 2 hours before noon. The reverse was true in the afternoon. The sampled branches lower than the tenth whorl were poorly illuminated throughout the day except for a brief period early in the afternoon.

We used the diurnal changes in radiation to establish the relation between radiation and resistance. In Fig. 10A the resistance in upper foliage of untreated trees is identified by solid symbols and establishes a standard response to radiation, which is the lower, solid curve. The resistance changed little over a wide range of radiation, increasing markedly only when radiation fell below 0.2 cal cm^{-2} min^{-1}.

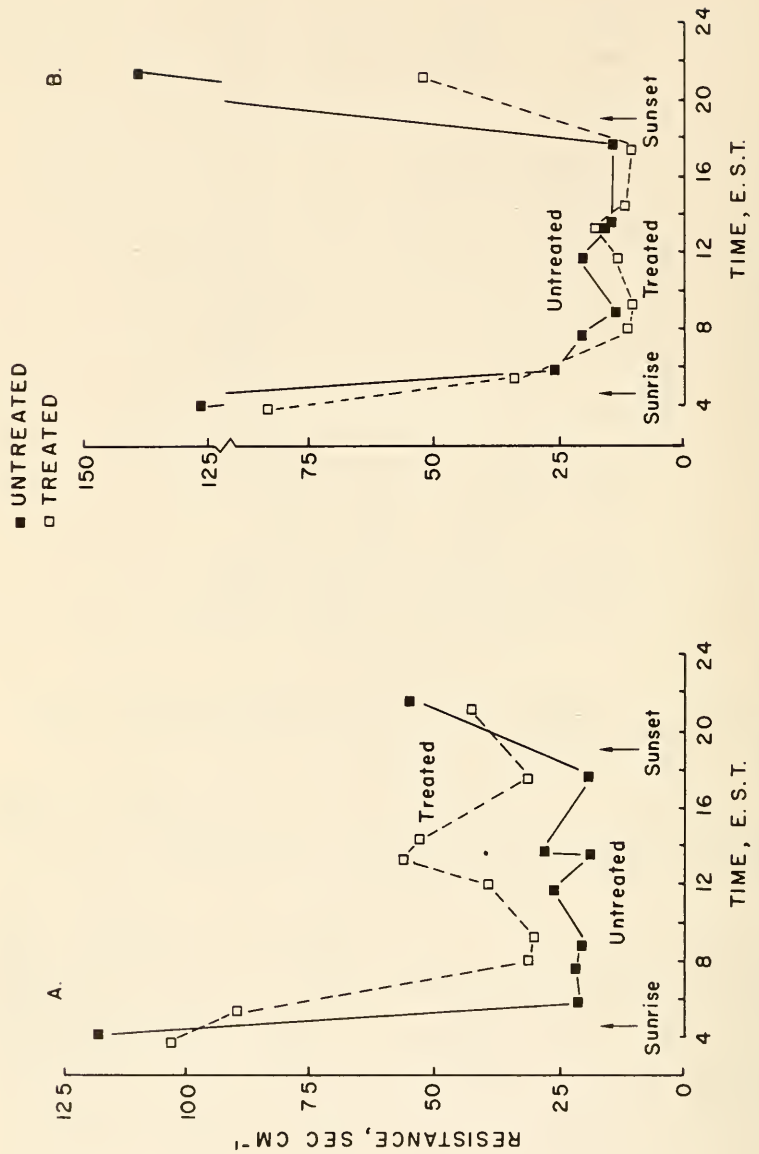

Fig. 8. Diurnal variation in stomatal resistance in untreated (■) and PMA treated (□) trees on 26 to 27 July 1967. A, 1-year-old fascicles; B, newly-emerged fascicles.

The behavior of stomata in the lower foliage is illustrated in Fig. 10B and can be compared to the standard response which is reproduced from Fig. 10A. The resistance is considerable in the lower foliage both because radiation is usually dim and because resistance is greater at the same radiation. Nevertheless, the stomata in lower foliage are functional and do open somewhat. The greater resistance of stomata in

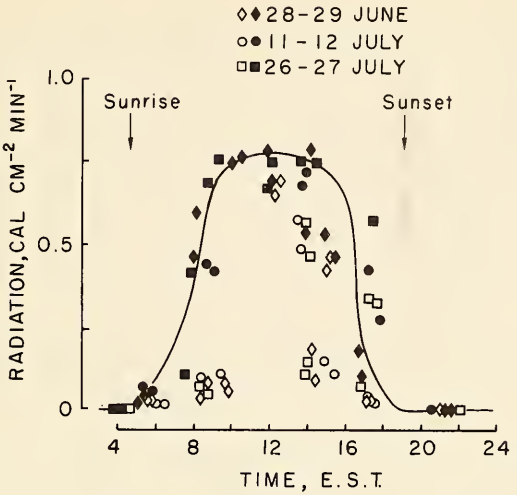

Fig. 9. Diurnal variation of omnidirectional radiation of the upper (closed symbols) and lower (open symbols) foliage in 1967.

lower foliage has been observed in other plants (Turner, 1969; Monteith and Bull, 1970; Turner and Incoll, 1971).

PMA, like location in the canopy, also alters the response of stomata to radiation. Thus, treated stomata open and close with changing light, but they do not open as widely as do untreated ones (Fig. 10A).

Water is another determinant of stomatal resistance, and its effect can also be seen in the diurnal course. Since the next chapter is devoted to plant hydration, however, the effect of water upon stomata is examined there, and we now turn to the seasonal course of stomatal resistance.

The seasonal variation in stomatal resistance can be seen from the measurements of stomatal resistance in the untreated trees obtained on several dates between early June and late October 1967. Prior to the emergence of the new fascicles, the resistance of the year-old fascicles was 11 to 15 sec cm^{-1}, but after the emergence of the new fascicles the resistance of the year-old fascicles increased to 19 to 22 sec cm^{-1} (Fig. 11). Upon emergence, the new fascicles had a resistance half that in the year-old ones for two reasons: those newly-emerged shaded the older ones, and the new fascicles had a lower resistance than the fully exposed year-old ones.

The resistances of both the new and year-old fascicles remained reasonably constant from July to early September, but then both increased in late October. Since the observations were restricted to the hours when radiation changed little (Fig. 9) and were generally restricted to days with clear or hazy sunshine, this constancy was expected. By October the air temperatures were 5C lower than those in September and 11C

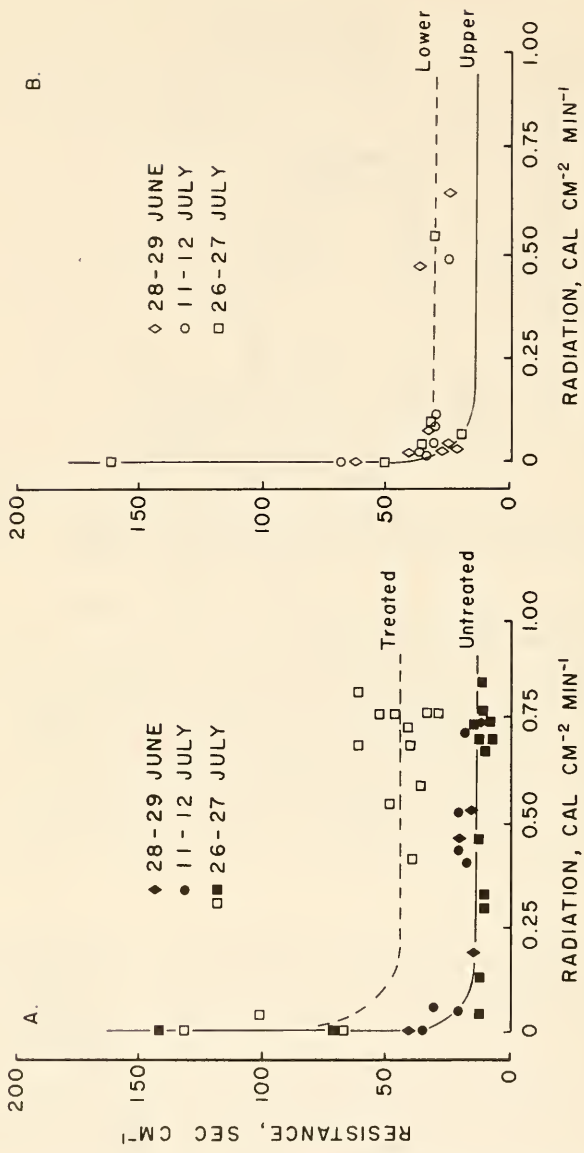

Fig. 10. Effect of radiation on stomatal resistance on three dates in 1967. A, in the upper foliage of untreated (closed symbols) and PMA-treated (open symbols) trees; B, in foliage from the upper six whorls (from A) and from whorls below the tenth (open symbols).

lower than those in July; we presume that the increase in resistance on the final sampling date occurred because of the cool soil and air temperatures prevailing by this date (Stalfelt, 1962).

We have already seen how PMA increased the stomatal resistance of the 1966 needles during daylight; we now follow its effects throughout the season. As observed with other species (Keller, 1966; Davenport, 1967), the effectiveness of PMA in closing stomata was temporary. On

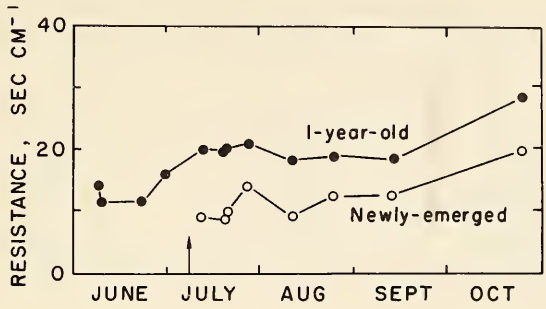

Fig. 11. Seasonal trend of stomatal resistance in newly-emerged (○) and 1-year-old (●) untreated foliage. Arrow indicates the approximate date of emergence of new needles.

23 June and 7 July 1966, infiltration of the organic dye was greater in untreated than treated needles, but thereafter no evidence of stomatal shrinkage could be found on either the newly-emerged or year-old needles.

In 1967, regular observation with the porometer showed that the effectiveness of PMA was greatest immediately after spraying, but it quickly diminished (Fig. 12) so that one month after the first spray the difference in stomatal resistance between the treated and untreated trees was no longer statistically significant. The second spray of 1967 again increased the resistance of the year-old needles. This second treatment with PMA increased the resistance more than the first so that on the day after spraying the treated needles had a resistance 2.5 times that of the untreated ones. This renewed difference also declined with time, but even at the end of the sampling period, some three months after re-spraying, the resistance of the treated needles was still 25% greater than the untreated, a difference which was statistically significant ($p \leq 0.001$). However, the PMA failed to close the stomata of the newly-emerged needles (Fig. 12), as observed earlier (Fig. 8B).

Simple wetting tests suggested that our inability to change the stomatal resistance of the newly-emerged needles was caused by inadequate wetting of the foliage. Therefore, in 1968 the water insoluble Triton B-1956 was replaced by the water soluble Triton X-100 wetting agent. Although adding Triton X-100 to the PMA significantly ($p \leq 0.05$) increased the stomatal resistance of the newly-emerged needles from 8.0 to 9.5 sec cm^{-1} in trees at the first plantation and 12.7 to 15.9 sec cm^{-1} at the second plantation, this was a small increase compared to that observed in older needles. Furthermore, the effectiveness upon new needles of PMA with Triton X-100 disappeared within three weeks (see Table 9).

We noted earlier that the smaller resistance of the newly-emerged fascicles, relative to the year-old fascicles, persisted throughout 1967 until the final sampling on 25 October. When first sampled on 4 June

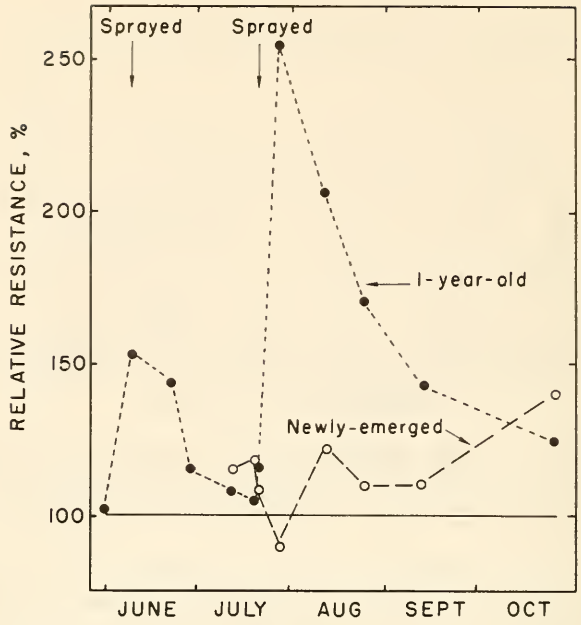

Fig. 12. Seasonal trend of stomatal resistance of newly-emerged (○) and 1-year-old (●) needles treated with PMA, relative to the stomatal resistance of the untreated trees.

1968, the 1966 needles still had a higher resistance of 12.0 sec cm^{-1} compared to the 9.6 of the 1967 needles, but the difference could not be substantiated statistically. To understand the effect of age better, the stomatal resistance of needles from different years was also studied on 20 to 21 June 1968 (Table 10). Stomatal resistance of untreated needles increased with age, with the greatest increase between the 0- and 1-year-old foliage (Tables 9 and 10). These observations from the second site

Table 9. Stomatal resistance (sec cm^{-1}), with standard error, of foliage with different years of origin, one day and three weeks after the second spray. The second plantation. Six replications.

Age of Foliage	Treatment None	First	Second	Both
		A. 16 July 1968		
Newly-emerged	13±1	.....	16± 1	.....
1-year-old	34±1	30±1	69±16	87±22
2-year-old	37±4	40±6	70±10	118±13
3-year-old	38±2	50±9	107±13	293±13
		B. 8 August 1968		
Newly-emerged	12±1	.....	12± 1	.....
1-year-old	26±2	43±3	30± 4	40± 4

Table 10. Stomatal resistance (sec cm^{-1}), with standard error, of untreated and treated foliage of different ages on 20 and 21 June 1968. Nine replications.

Age of foliage	Treatment	
	Untreated	Treated
Newly-emerged	11±1	.....
1-year-old	17±2	33± 3
2-year-old	22±2	40± 6
3-year-old	23±2	65±10
4-year-old*	28±3	No foliage

* Four replicates only

were substantiated by similar observations at the first plantation. The differences cannot be entirely attributed to age since the older needles were presumably more poorly illuminated than the younger ones; the difficult task of measuring the radiation receipt of needles of different ages was not undertaken.

Tables 9 and 10 also show the effect of age upon the effectiveness of PMA: the older the needles, the more effective the spray in closing the stomata. The observations in Table 10 were made in the second plantation, and the foliage had received only a single application of PMA 18 days earlier. The second spraying of the foliage also had a greater effect on the older needles (Table 9). Although the stomatal closure caused by the first spray was no longer evident when the second spray was applied, the first treatment evidently predisposed the stomata to greater closure on re-spraying. Moreover, the effect of a double spray persisted longer than a single spray as revealed on 8 August (Table 9); by this date the early senescence of those needles sprayed on 4 June was already evident as an increased stomatal resistance.

Having seen the effect of light or hour, season and PMA upon stomatal resistance, we next examine water potential in the foliage, which both affects stomatal resistance and is affected by the resistance.

Chapter 5
WATER POTENTIAL IN THE FOLIAGE

If the demand for water for transpiration becomes excessive, or the resistances to flow in the pathway of water movement within the plant or soil become too great, the deficit of water in the foliage can reduce leaf turgor to the point at which stomata close. Thus we studied the development of water potential in the foliage, called foliage potential for short, and studied its effect on stomatal aperture.

The development of the pressure chamber (Scholander *et al.*, 1964, 1965) provided a simple method for measuring foliage potential in the field. The technique employs a strong, stainless steel chamber that can

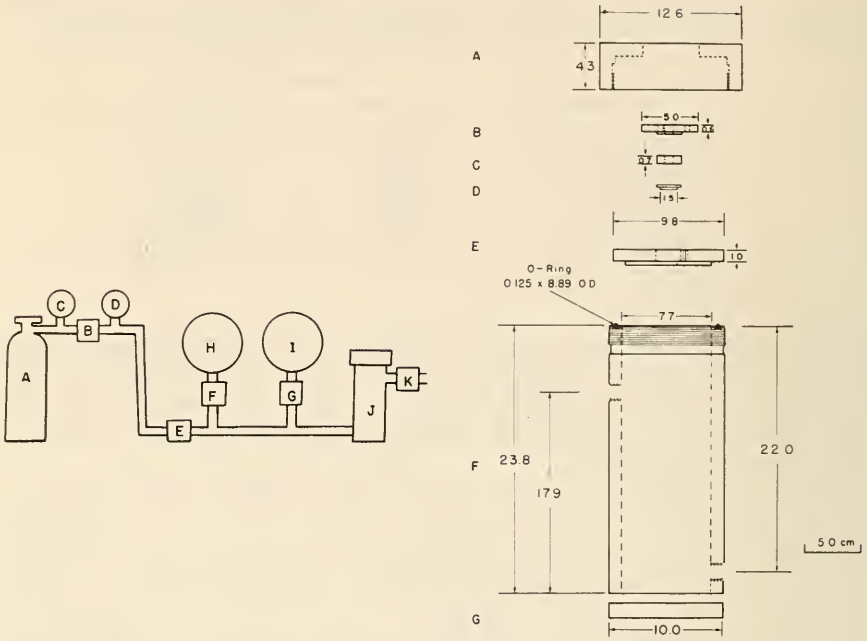

Fig. 13. Pressure chamber system.
Left. Schematic diagram of system. A, cylinder of nitrogen gas; B, reduction valve; C, pressure gauge (0-210 kg cm^{-2}); D, pressure gauge (0-70 kg cm^{-2}); E, metering valve; F, G, shut-off valves; H, pressure gauge (0-70 kg cm^{-2}); I, pressure gauge (0-21 kg cm^{-2}); J, pressure chamber; K, exhaust valve.
Right. Detail of pressure chamber. Front view. A, cover; B, D, interchangeable sealing plates; C, compression gland; E, chamber top; F, cylindrical chamber with inlet (lower) and exhaust (upper) ports; G, chamber base, which is welded to F. Dimensions are in centimeters.

withstand pressure greater than 70 kg cm^{-2}, a cylinder of nitrogen gas under pressure, pressure gauges and a reduction valve (Fig. 13); the system has been fully described by Turner *et al.* (1971). The cut stem of a needle-bearing twig is sealed into the top of the chamber. Pressure from the cylinder of nitrogen is applied to the twig until the meniscus of the xylem sap returns to the cut surface, and the balancing pressure is noted (Fig. 14). Boyer (1967), Kaufmann (1968 a, b) and De Roo (1969, 1970) have shown that the balancing pressure is nearly equivalent to the foliage potential measured with a thermocouple psychrometer for a range of species. H. C. De Roo of The Connecticut Agricultural Experiment Station confirmed that this was also true for red pine.

The diurnal pattern of potential in the upper foliage during three 24-hour periods of clear weather is presented in Fig. 15. The potentials encountered on the three days were not identical, but they all show a de-

Fig. 14. Ben-Ami Bravdo and Dwight B. Downs using the pressure chamber at Voluntown.

creasing potential in the morning with a slow increase in water potential after 1400 hr E.S.T. as observed by others in different species (e.g. Waring and Cleary, 1967). At sunset the foliage potentials were still as low as —6 to —8 bars, but the trees continued to recover overnight and had reached potentials as high as —2 bars by daybreak. The minimum foliage potential observed during the three days was —14.7 bars.

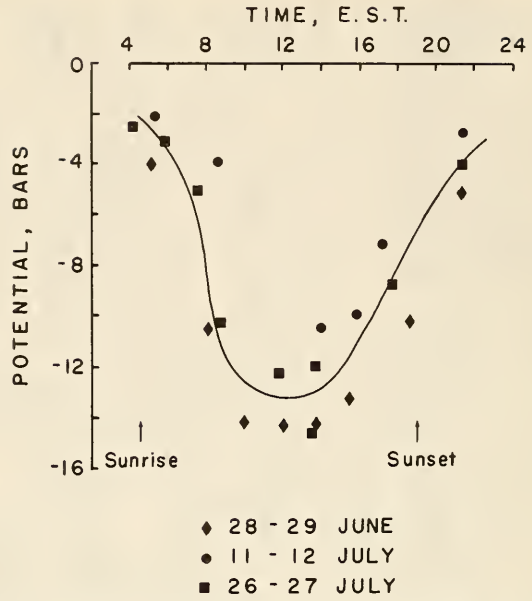

Fig. 15. Diurnal variation in the water potential of foliage from the upper six whorls of untreated trees on three dates in 1967.

If we select one of the three periods, we see that the water potential of the lower foliage was higher (less negative) than that in the upper foliage at all times during the day (Fig. 16); the data from the other

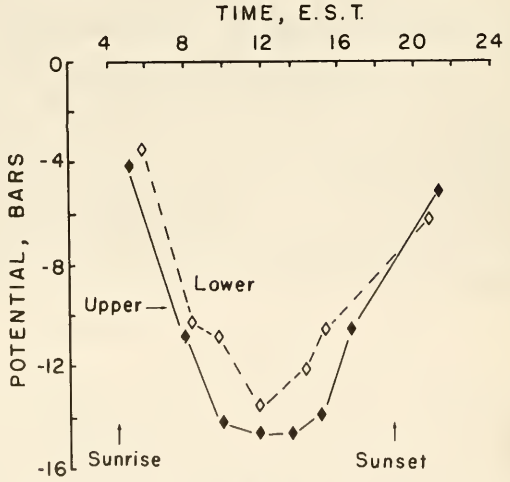

Fig. 16. Diurnal variation in the potential of foliage from the upper six whorls (◆) and foliage from below the tenth whorl (◇) on 28 to 29 June 1967.

days verified this. Since we have already seen that the radiation incident upon the lower branches was dim (Fig. 9) and the stomata did not open as widely in the lower as in the upper foliage (Fig. 6), it is not surprising that foliage potentials were less negative in the lower than in the upper foliage. This potential difference with height, of course, drives the transpiration stream in red pines as it does in other trees (Scholander *et al.*, 1964).

Next we examine whether stomatal resistance was affected by a decrease in water potential. To do this stomatal resistance was related to the potential of the upper foliage on those occasions when the radiation was greater than 0.2 cal cm^{-2} min^{-1}, i.e. when stomatal resistance was not affected by dim light (Fig. 10A). The range of potentials encountered when radiation was above 0.2 cal cm^{-2} min^{-1} was —4 to —15 bars. Fig. 17 shows the newly-emerged needles were sensitive to water stress; the stomatal resistance doubled from 7.5 to 15 sec cm^{-1} as the foliage potential decreased from —4 to —15 bars ($r^2 = 0.52$). However, the year-old needles, as best we can tell from the variable data, were unaffected. Thus, if PMA increases the foliage potential, as well we might expect, this should cause the stomata of the newly-emerged foliage to open and thus act against the stomatal closing properties of the chemical itself. This might be an additional reason for the ineffectiveness of the spray on the newly-emerged foliage (Figs. 8B, 12).

During the season the mean foliage potential of the unsprayed trees varied between —7 and —14 bars (Fig. 18A). Any seasonal trend that there might have been was obscured by the variability in evaporative conditions encountered. Evaporation from a Class A pan 3 km away at the Pachaug State Forest Nursery varied from 2.3 to 6.9 mm on the days that foliage potentials were measured; the foliage potentials were roughly correlated with the daily evaporation (Table 11).

We also tested whether the leaf area had an effect on the water potential developed by the foliage. On 6 and 7 May 1969, when the difference in leaf area between the treated and untreated trees was greatest but the leaf porosity was similar, the mean foliage potential in 8 un-

Table 11. Daily pan evaporation and mean foliage potential of unsprayed trees at various sampling dates throughout the 1967 season.

Date	Foliage Potential, bars	Pan Evaporation, mm
June 28	—14.1	6.9
July 12	— 6.8	2.3
18	— 8.7	3.6
19	— 8.6	1.8
26	—13.1	4.8
August 11	— 8.8	2.3
24	—13.0	3.3
September 12	—13.4	4.3

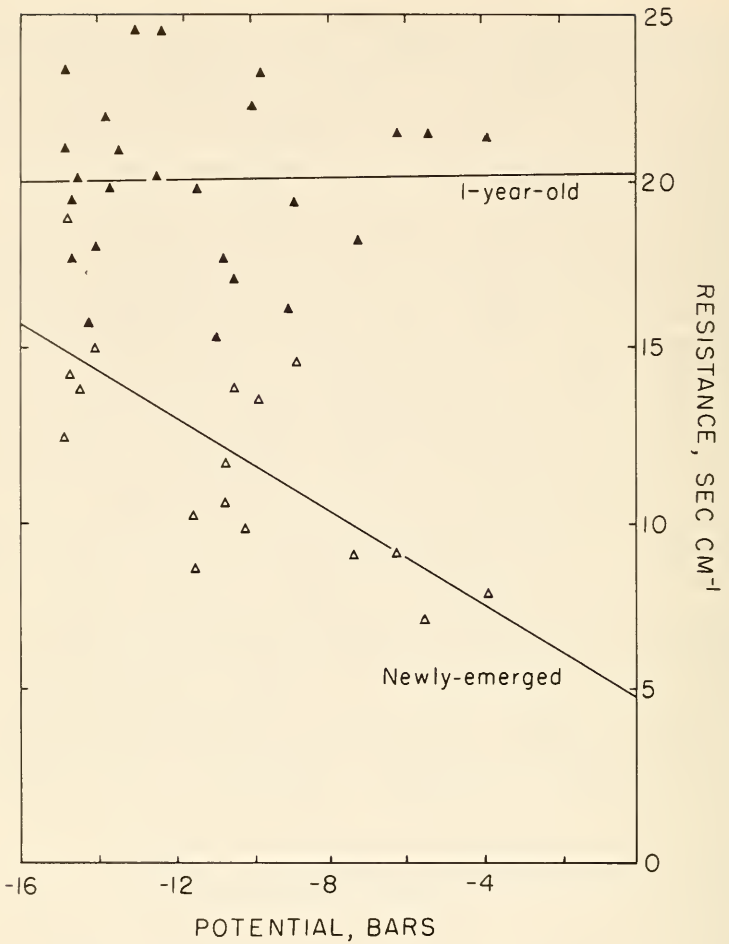

Fig. 17. Effect of foliage potential on the stomatal resistance of the newly-emerged (△) and 1-year-old (▲) needles when the radiation exceeded 0.2 cal cm^{-2} min^{-1}.

treated trees was —13.4 bars whereas in the treated trees it was 2 bars higher at —11.4 bars. Clearly, the shedding of one third of the fascicles (Table 5) reduced the stress on the foliage.

PMA increased stomatal resistance in year-old needles (Fig. 8A) and this increased the foliage potential (Fig. 19). During daylight the increase in foliage potential from treatment with PMA was greater in the lower branches than the upper branches: in the upper branches it was increased by a quarter, whereas in the lower branches it was increased by half. This suggests that PMA, which was equally effective in closing stomata of upper and lower foliage, slightly increased the needle temperature of the upper foliage that received the direct insolation. Such

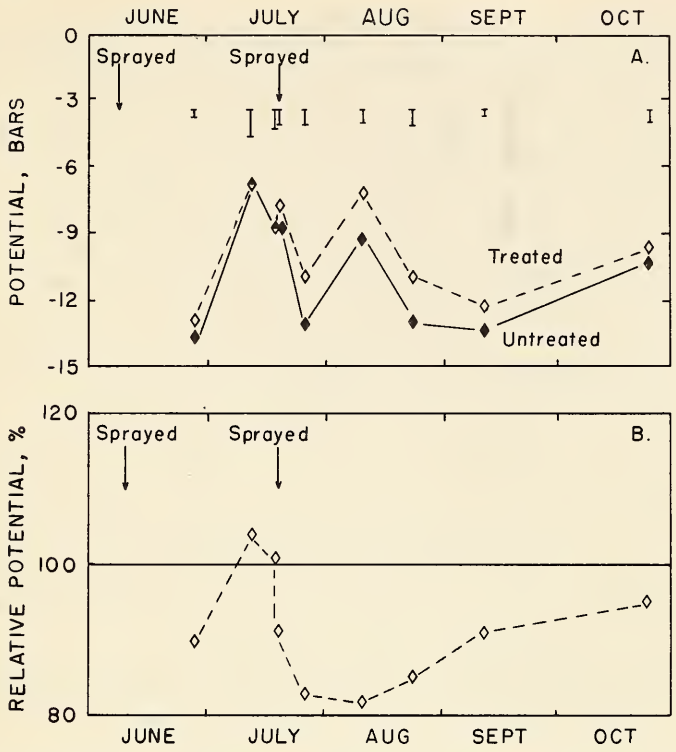

Fig. 18. Seasonal trend in foliage potential, A, in untreated trees (◆) and trees sprayed with PMA (◇); B, in treated trees relative to the unsprayed controls. The bars denote the standard error of difference.

a rise in temperature would increase evaporation by increasing the gradient of water vapor from within the leaf to the atmosphere, and thus partly compensate for the decrease in stomatal width. That this compensation was only partial is clear from the actual increases in foliage potential.

We have now seen from the diurnal study that PMA increased the foliage potential throughout the daylight hours. Also we noted that the effect of PMA on stomatal closure was transient (Fig. 12). Therefore, we expect that the effect of PMA on foliage potential will also be transient. This was indeed found to be the case. Foliage potential was first measured on 28 June 1967, 20 days after spraying with PMA. At that time, the potential of the sprayed foliage was a significant ($p \leq 0.05$) 1.5 bars higher than in the unsprayed trees (Fig. 18A). However, by the time of the subsequent sampling the effect of PMA was no longer evident. Spraying the trees again on 19 July 1967 increased the potential of the affected foliage (Fig. 18B), but the effectiveness of the PMA

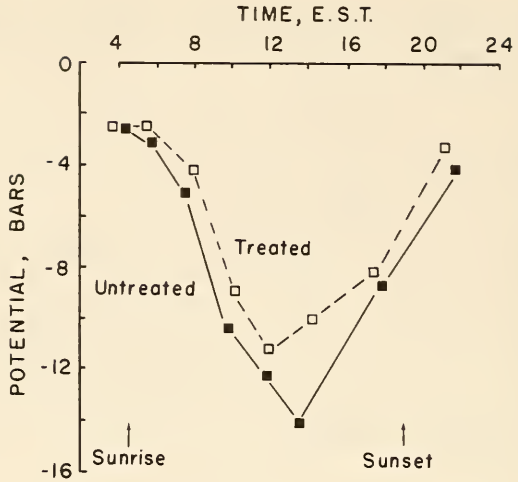

Fig. 19. Diurnal variation in potential of untreated (■) and PMA-treated (□) foliage on 26 to 27 July 1967.

declined with time until the 0.5 bar difference at the final sampling on 25 October was no longer statistically significant.

These variations in foliage potential are reflected in the diurnal shrinkage of the boles or trunks of the trees, which is examined in the next chapter.

Chapter 6

BOLE CONTRACTION, A REFLECTION OF WATER POTENTIAL

The water in the xylem of the tree trunk or bole is under tension, and this tension manifests itself in a contraction of the bole that can be measured. We have shown in the preceding chapter that several bars of pressure must be applied to the outside of an excised shoot to replace the tension in the xylem that was previously attached to the shoot, and one should not be surprised to find that the change from the small 3 bars of tension at dawn to the 15 bars of tension at midday cause nearly 100 microns or 0.1 mm of shrinkage of the sapwood and phloem of a bole. Since this shrinkage can be easily measured on many trees, it is our most frequent and widely replicated measurement of the water status of the trees.

Dendrometers for the measurement of radial growth and diurnal shrinkage of boles have taken two forms, *viz:* (a) band dendrographs in which changes in the length of a metal band around the bark of the tree at a fixed height are recorded, and (b) dial gauge dendrometers in which the distance between the outer surface of the bark and a fixed

screw mounted in the heartwood is measured with a sensitive depth gauge. MacDougal (1921) described several of the early band dendrographs and used a modified version himself for continuous recording of tree perimeters. The introduction of the dial gauge dendrometer can be traced back to Reineke (1932); Daubenmire (1945) improved the earlier model by replacing the single hook screwed into the heartwood with three screws. Both types of dial gauge dendrometer have also been modified for continuous recording (Fritts and Fritts, 1955; Klemmer, 1969). Tree bands are sensitive to temperature fluctuations and insensitive to shrinkage. On the other hand, growth and shrinkage do vary on different sides of the tree, and thus bands give a better average of total bole growth than does the dial gauge (Bormann and Kozlowski, 1962).

The dendrometer that we employed is illustrated in Fig. 20. First, the loose bark is removed from a bole at a height of 140 cm. Then a brass ring is cemented to the sound bark. Next, three nails are driven into the heartwood of the tree on the perimeter of a circle around the ring (Fig. 20A). The movement in and out of the ring relative to the heads of the nails reflects the shrinkage of the sapwood and phloem and is measured with the depth gauge or "dendrometer" shown in Fig. 20B. This particular dendrometer was developed in earlier investigations by B. Bravdo and R. M. Samish and introduced into the Voluntown experiments by Bravdo.

Dendrometer stations, i.e. rings and nails, were established on six trees within each of the 16 plots, 8 treated and 8 untreated, of the first plantation and on each of the 114 trees of the second plantation. In 1968 four plots at the first plantation that were infected with butt rot were discarded; this reduced the number of dendrometer stations from 96 to 72. Generally measurements were taken near 1300 hours E.S.T. on the first day and at 0700 and 1300 hours on the second day. The shrinkage on the first day was calculated as the difference between the first two of the trio. About an hour was required to complete all observations in a plantation, and treated and untreated trees were measured alternately.

The reproducibility of the measurements, including both the errors of measurement and the variability of shrinkage among trees can be judged by the standard errors of the mean shrinkages observed in the first plantation on 32 occasions in 1967. From time to time a ring would become loose and a measurement be omitted during its replacement; thus the number of treated or untreated trees measured fell as low as 38 in the first set of observations, but usually the number of observations averaged was near the ideal of 48. The mean shrinkage on the 32 occasions ranged from a low of 5 to a high of 112 microns. The standard error of these means ranged from 1 to 4 microns. Thus differences as small as 10 microns between occasions or treatments were clearly significant.

The response of the shrinkage and the dendrometer indications to the

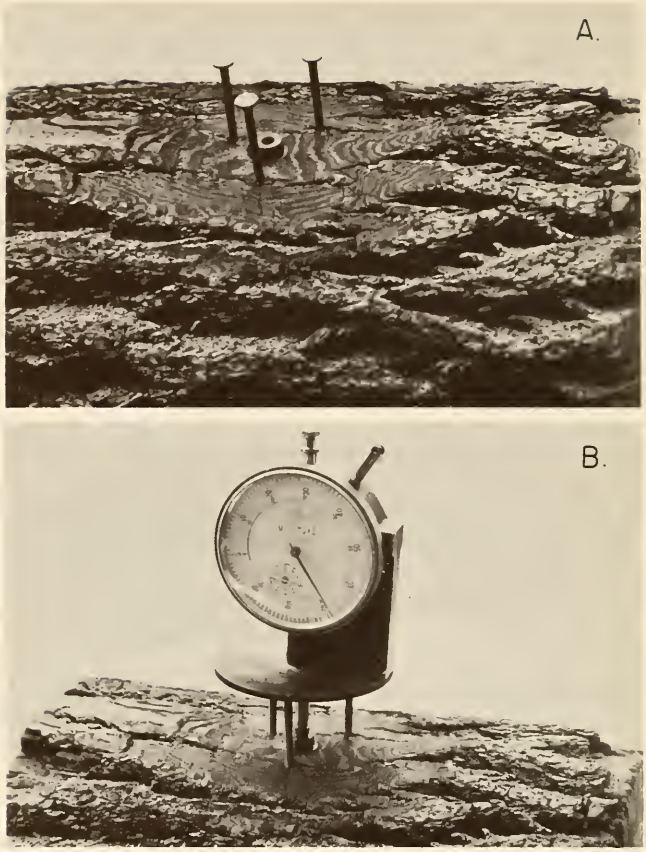

Fig. 20. A, Dendrometer station; B, Dial gauge dendrometer, used to measure radial growth and bole contraction.

weather can be seen in Fig. 21. Since the shrinkage is attributed to the excess of evaporation from the foliage above the supply from the roots, it should increase with evaporation. On 21 days when dendrometer measurements were made in 1967, the evaporation from a Class A pan was measured between mid-morning and the following morning at the Pachaug State Forest Nursery, 3.5 km from the first plantation. The shrinkage of the boles on these 21 days is plotted in Fig. 21 as a function of the evaporation. Clearly the shrinkage increases about 1.2 microns with each 1 mm increase in evaporation; the correlation coefficient is 0.70.

The shrinkage of the boles should also be related, perhaps more closely, to the radiation. That is, the evaporation from the foliage is affected by both the warming of the foliage and the opening of stomata that is increased by sunlight, while evaporation from a pan may be greatly affected by the nighttime humidity and ventilation that have

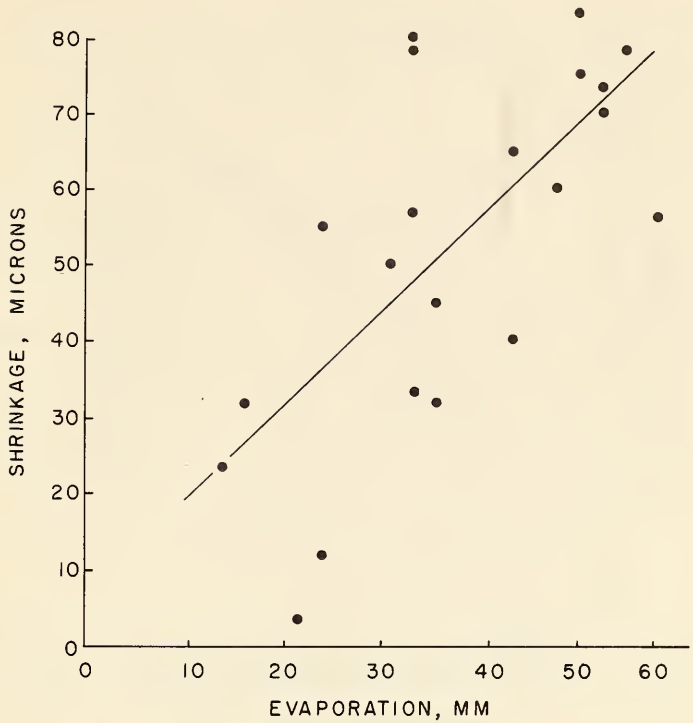

Fig. 21. Relation between shrinkage of boles in untreated trees at the first plantation and evaporation on the following day from a pan at the Pachaug State Forest Nursery, 3.5 km from the plantation.

little effect upon the foliage when stomata are sealed by darkness. Thus it is not surprising to find in Fig. 22 that the shrinkage is correlated even more closely (r is 0.75) with radiation than with evaporation. The radiation on the 25 days is the insolation indicated by a bimetallic pyrheliograph (Belfort Instrument Company, Baltimore, Md.) also at the Pachaug State Forest Nursery.

The effect of the weather was also evident in the diurnal course of shrinkage. On four days in 1967 the shrinkage of trees on half of the plots in the first plantation was measured at intervals throughout the day. Fig. 23 shows the course on cloudy 22-23 June and clear 26-27 July. The maximum shrinkage on the clear day was just twice that on the cloudy day. Maximum shrinkage occurred between 1400 and 1600 hours E.S.T., and minimum shrinkage was observed between 0600 and 0700 hours E.S.T. as observed previously by Haasis (1934). Thus bole contraction 140 cm from the ground lagged 3 hours behind the radiation incident upon the upper foliage (Fig. 24) except that the bole was still some 20 microns smaller than its maximum diameter 3 hours after sunset.

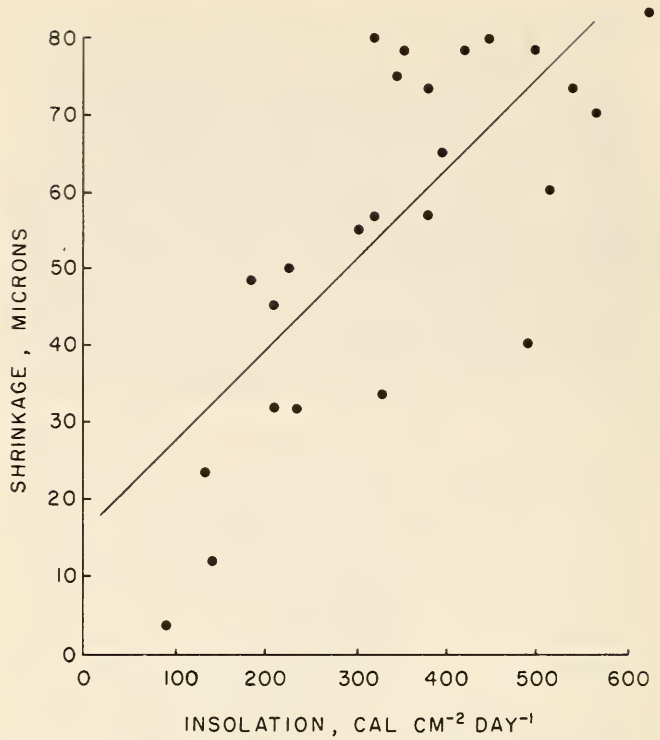

Fig. 22. Relation between bole shrinkage of untreated trees at the first plantation and insolation measured with a bimetallic pyrheliograph at the Pachaug State Forest Nursery, 3.5 km from the plantation.

The relation between bole contraction and incident radiation presumably arises from its effect on stomatal opening and heating of the foliage that, in turn, affect the water potential of the foliage. Indeed, Worral (1966) showed that a good correlation between diameter and water status did exist under equilibrium conditions. However, our first attempt to correlate bole shrinkage and foliage potential under the dynamic situation of the field was not entirely successful (Fig. 25A). Clearly, bole contraction at 140 cm from the ground lagged behind the potential of the upper foliage on the same trees; a 2 hour lag was evident (Fig. 25B). The lag is, of course, an interesting function of the relative water potentials of atmosphere and soil, relative conductivities of soil and plant organs and water capacity of the bole. This could be expressed more explicitly in a simulator or model. Unfortunately, however, the size of the various parameters is so poorly known that building the simulator seems premature. The important thing is that bole shrinkage reflects foliage potential, and the lag in bole shrinkage demonstrates a

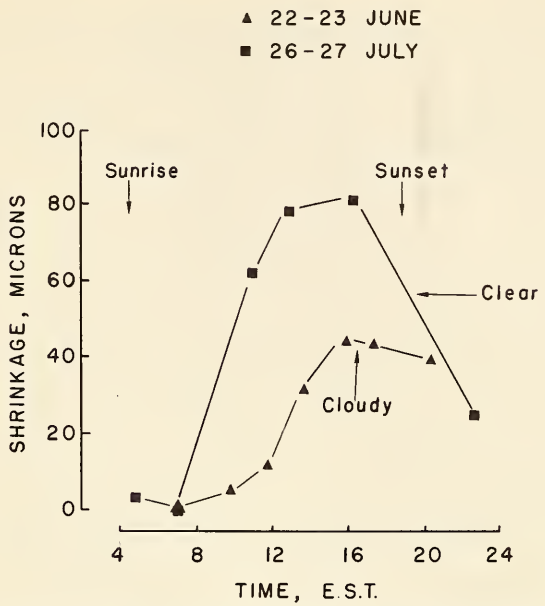

Fig. 23. Diurnal variation in bole shrinkage in unsprayed trees on a clear (■) and a cloudy (▲) day in 1967.

considerable reservoir of available water within the foliage and bole of the tree (MacDougal, 1921).

We next examined whether the shrinkage was a function of the nature of the trees. Did shrinkage vary with trunk diameter or the expansion of bole? The 14 linear correlation coefficients between trunk diameter and the shrinkage on seven occasions in 1966 in the treated and in the untreated trees were calculated. Only one of the 14 coefficients attained the 5% significance level, leaving us convinced that big and little trees shrink about the same amount. Since roots, xylem and crown grow in about the same proportions, it is not surprising that big stems with big crowns shrink no more than little stems with little crowns.

Also the relation between the shrinkage and the growth of the trees was sought since it seemed reasonable that a rapidly growing tree might have more tissue that could be shrunken by the diurnal drying than would a slowly growing tree. Thirty-seven untreated trees had sound dendrometer measurements of both expansion from 10 May to 6 July 1967 and shrinkage on 6 July. The expansion varied from 170 to 1860 microns and the shrinkage from 30 to 100 microns. The correlation between shrinkage and expansion in both these trees and the corresponding treated ones was, unfortunately, negligible. Thus the shrinkage of the boles is a function of weather and foliage potential but not of the range of the bole size and expansion encountered in the Voluntown plantations.

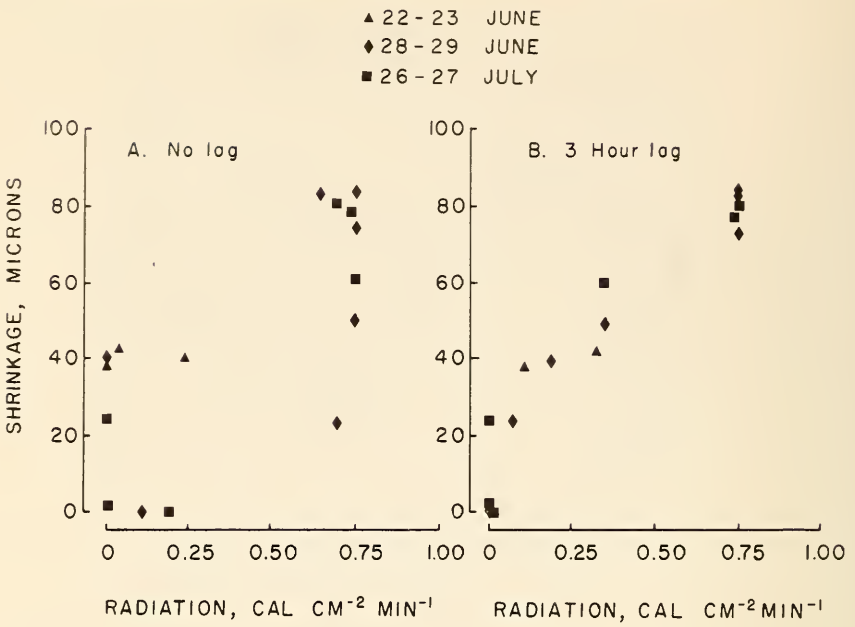

Fig. 24. Relation between bole shrinkage and radiation measured near the foliage for three dates in 1967. A, shrinkage related to radiation observed at the same time; B, shrinkage related to the radiation observed 3 hours earlier.

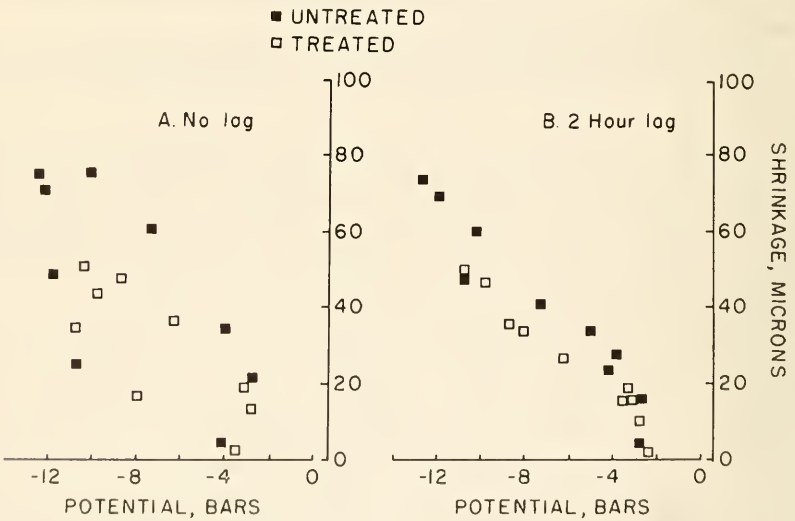

Fig. 25. Relation between bole shrinkage and foliage potential in PMA-treated (□) and untreated (■) trees. A, shrinkage related to potential observed at the same time; B, shrinkage related to the foliage potential 2 hours earlier.

Finally, we examined the effect of PMA on shrinkage. Since the relation between bole contraction and foliage potential was the same in PMA treated and untreated foliage (Fig. 25), we can confidently use our observations of the effect of PMA on bole contraction to provide a broad demonstration of the effect of stomatal control on the foliage potential of the forest. The relation between shrinkage in the treated and untreated trees was observed in three ways: first, for a few exemplary occasions; second, the ratio between the two for entire seasons; and finally, the change in the ratio during a season.

No observations were made before the first spray in 1966, but shortly afterward the relation between the two sorts of trees was typified by shrinkage of 95±4 microns in the untreated and 72±4 in the treated. By late August, however, the difference had disappeared. Before the first spray in 1967, shrinkages of 92±3 and 82±4 were observed in untreated and treated trees; but after two sprays, they became 75±3 and 57±3, for example. In 1968, a difference between the two was evident both before and after the sprays. Finally, in 1969 when the trees were untreated, the shrinkages were 75±4 and 66±4 on 11 July.

In the second plantation, three observations were made before the first spray, confirming the equality of shrinkage in the two sets of trees. After spraying, shrinkages of 94±5 and 84±4 represented the untreated and treated. The second spray had no detectable effect.

The ratio for an entire season can be seen in Fig. 26. The season is 1967, when observations were most numerous. The average ratio, shown by the line, is 0.75. The observation before spraying is the point to the left of the curve and at the top, showing that the trees to be treated a second year shrank fully 90% as much as the untreated. The point to the right of the curve near the top is the first observation after spraying, when the ratio fell to only 0.72.

The mean ratios for all occasions in the four years are presented in Table 12. The results from the first plantation seem easily interpreted. The relative shrinkage of the treated trees diminished over the first three years as treatment was repeated, stomata shrank, and especially in 1968, foliage was diminished. Then, with no spraying in 1969, the formerly treated trees shrank more nearly like the untreated ones. In the second plantation the first spray decreased shrinkage to 90% in the absence and 87% in the presence of a second spray. Surprisingly, it persisted into the second year.

The final view of the diurnal shrinkages is of their annual courses, which reveal the onset and disappearance of treatment effect. These courses are plotted in Fig. 27. Occasions when the untreated trees shrank less than 40 microns were discarded because small values can cause erratic jumps in the ratios. Then the ratios of treated to untreated were calculated and plotted in the Figure together with the best fitting, two-term polynomial, relating ratio to date.

In 1966 the effect of treatment and its disappearance towards season's end are clearly visible. In 1967 the single observation before treatment

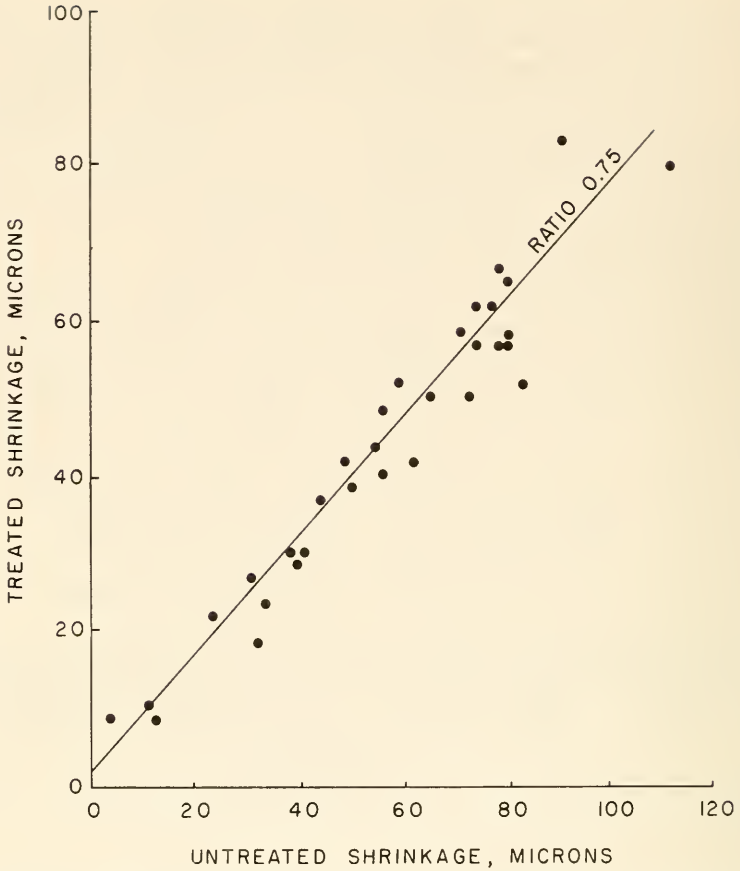

Fig. 26. Relation between bole shrinkage in PMA-treated and untreated trees at the first plantation in 1967.

can be seen as the high ratio at the left, but it scarcely influenced the polynomial curve; the treated trees then shrank less than the others throughout the season. In 1968, the three observations before spraying influenced the polynomial curve, and the onset and decay of the effect of treatment are clearer than in 1967. Finally, in 1969 when sprays were omitted, the formerly sprayed trees continued to shrink less than those that were never treated; but the diminution in shrinkage was less than in the years of spraying. We have no reason not to ascribe the small diminution of shrinkage in 1969 to the lesser amount of foliage following five sprays.

Our observations of the daily shrinkage of the treated trees, whose transpiring stomata had been somewhat shrunk by PMA, can be summarized quickly. Treatment was promptly followed by less shrinkage, and in successive years of treatment the decreased shrinkage persisted

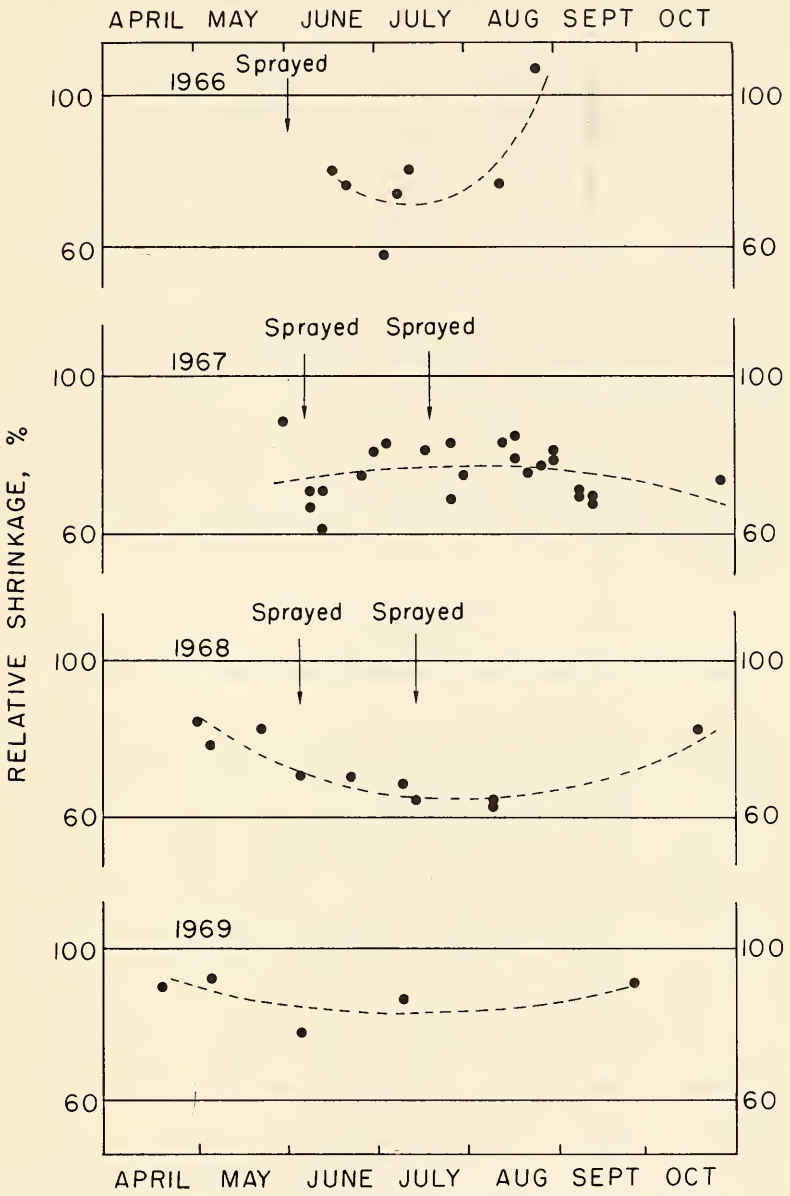

Fig. 27. Seasonal course of daily bole shrinkage in treated trees relative to the shrinkage in untreated trees during the 4 years of observation.

Table 12. The annual mean ratios of diurnal shrinkages in treated trees to shrinkage in untreated trees.

Year	First Plantation		Second Plantation°	
	Number of occasions	Ratio	Number of occasions	Ratio
1966	8	0.82		
1967	32	0.75		
1968	14	0.71	12	0.90
1969	6	0.88	5	0.90

° Trees sprayed first time versus no spray.

further into the summer than did our evidence of stomatal closure. Finally, the decrease persisted slightly a full year after treatment, probably because of the loss of foliage removed by the repeated sprays.

In the next chapter we go on to show how the early morning observations with the dendrometer were used to measure the radial growth of the tree bole. In addition we observed the annual radial growth by means of increment cores and measured the extension of the internodes and needles.

Chapter 7

GROWTH OF THE BOLES, INTERNODES, AND NEEDLES

Growth is intrinsically interesting: we want to know whether the red pines in the two plantations behave in the normal pattern (Kienholz, 1934). Even more interest, however, attaches to learning whether treatment with the stomata-closing chemical materially decreased growth.

Two mechanisms for decreased growth following treatment with PMA can be postulated. First, and most subtle, stomatal shrinkage could obstruct the intake of carbon dioxide and hence photosynthesis and growth. This effect upon photosynthesis is, however, logically, and in fact in several plants, relatively less than the effect upon evaporation (Zelitch and Waggoner, 1962). Fig. 8 shows that evaporation from a needle is decreased by half or less, and Chapter 9 will show that evaporation from the plantation is decreased less than a tenth during an entire season. Hence growth is likely retarded little by the increased resistance to carbon dioxide intake following stomatal shrinkage.

The second mechanism of growth retardation by PMA is less subtle but undoubtedly more important: foliage became visibly chlorotic and fell following PMA treatment in June 1968. Traps revealed some defoliation as early as 1967. This damage to the already modest supply of foliage in the first plantation was bound to affect growth.

The growth of the trees was measured in two ways: the expansion of the boles or trunks and the elongation of the branches and needles. The

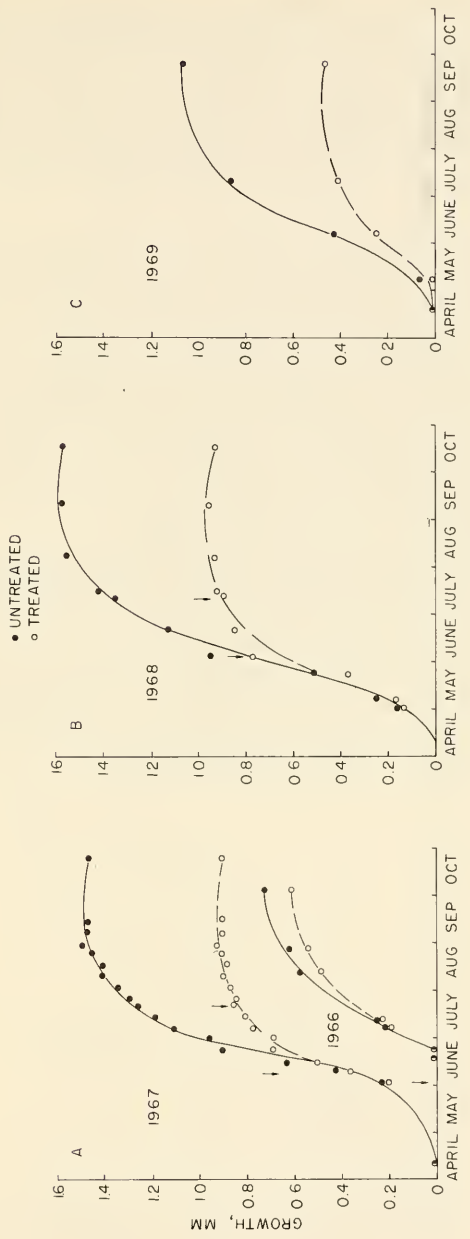

Fig. 28. Expansion of the boles of untreated (●) and PMA-treated (○) trees at the first plantation. A, 1966 and 1967; B, 1968; C, 1969. Arrows denote time of spraying with PMA.

expansion of the boles was measured by the day-to-day changes in the same dendrometer that was used to measure shrinkage from hour-to-hour, and also by cutting cores from the boles of the same trees at the same height (140 cm) as the dendrometer stations and measuring the annual growth of wood microscopically. We begin with the dendrometer observations, which have just been used in the preceding chapter, and follow the annual course of expansion of the bole as well as the annual total growth.

The courses for the first plantation for the four years of the experiment are shown in Fig. 28, parts A, B and C. The standard errors of the increase between two observations were generally 5 to 20 microns. The salient features of the annual course can be seen in 1967: the boles expand rapidly during May through August, and the wood beneath the dendrometer expands 1 to 1½ mm per year. Year 1966 provides the greatest departure from this pattern, but the smaller expansion is largely caused by the late beginning of observations in June rather than by the drought of that year. The greater growth in the second, more vigorous and younger plantation is illustrated in Fig. 29.

The increasing inhibition of growth by PMA is evident in Fig. 28. In the first plantation, the expansion of the treated trees was scarcely less than the untreated ones in the first year, 1966. After the second spray on 9 June 1967, however, the treated trees grew markedly less, ending the year with a third less expansion. The outcome of the third year was much the same. In the fourth year, although the trees were unsprayed, the formerly treated ones did have less foliage, and they grew only about half as much as untreated ones.

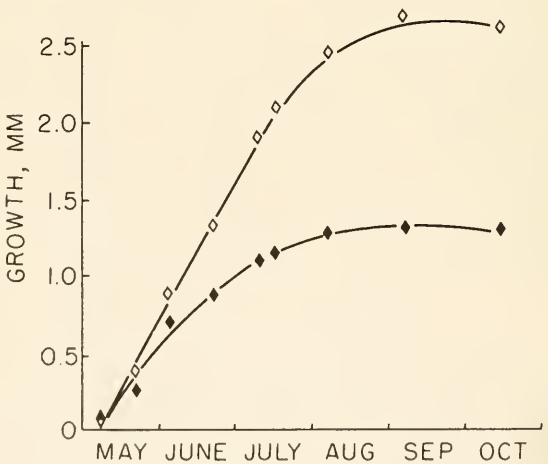

Fig. 29. Expansion of the boles of untreated trees at the first (◆) and second plantation (◇) in 1968.

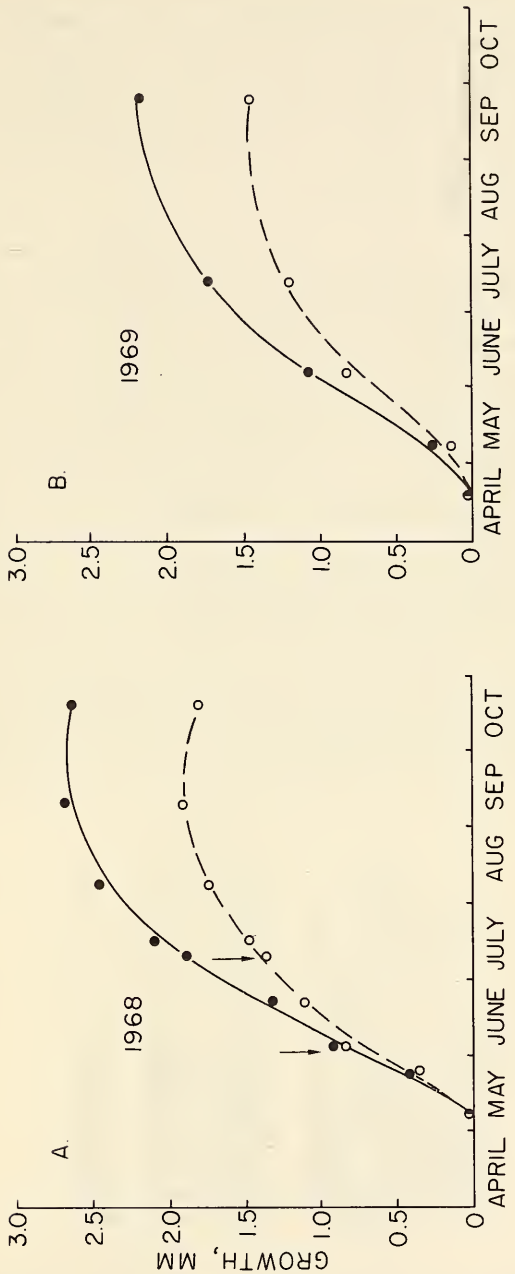

Fig. 30. Expansion of the boles of untreated (●) and PMA-treated (○) trees at the second plantation. A, 1968; B, 1969. Arrows denote time of spraying with PMA.

The outcome of the spraying of the second plantation revealed the effect of PMA more quickly, Fig. 30. That is, the increment immediately after the first spray was only 267±15 microns in the treated trees, while the untreated ones expanded 433±18 microns in 17 days. The second spray had no effect. At season's end the treated trees had expanded only 70% as much as the untreated ones. Next, the annual total, rather than course, of growth is observed in the thickness of new wood at the same height as the dendrometer stations.

From increment cores taken on 19 November 1969 the radial growth of the xylem, hereafter simply referred to as xylem growth, was observed for five years at the first plantation and three years at the second plantation. The normal year-by-year variation in the xylem can be seen from the untreated trees in Fig. 31; in all years except 1966, a year with lower rainfall and higher evaporation than average (Chapter 2), the xylem growth in the untreated trees was between 0.9 and 1.0 mm at the first plantation. Spring growth, characterized by large tracheids with light colored walls, and summer growth, characterized by small tracheids with dark walls, each comprised half the annual growth. The increment cores confirmed that the annual growth at the second plantation was twice as great as the annual growth at the first site (Fig. 32). But growth, primarily spring growth, declined progressively over the three years in the untreated trees, presumably as the canopy closed.

The xylem growth in the trees at the first plantation sprayed with PMA became progressively smaller in each succeeding year (Fig. 31), confirming the observations of the dendrometer. Both spring and summer growth were affected by spraying; spring growth was affected to a lesser extent than summer growth. Examination of the increment cores

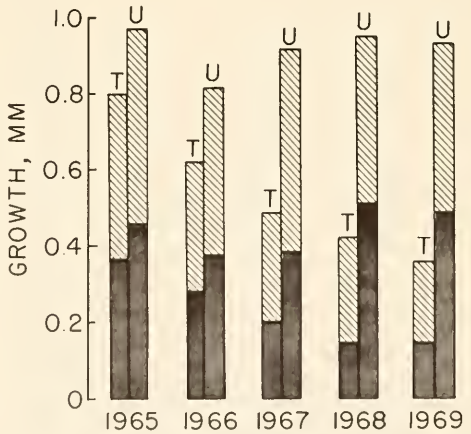

Fig. 31. Radial growth of the xylem in untreated (U) and PMA-treated (T) trees at the first plantation for the 5 years prior to sampling in November 1969. Hatching denotes spring growth and shading denotes summer growth.

also showed that the immediate reduction in bole expansion observed with the dendrometer after the first spray at the second plantation occurred in the xylem; spring growth was reduced considerably less than summer growth (Fig. 32). The immediate effect of the spray on summer growth presumably arose from the damage by this one spray (Chapter 3) and is not typical. Certainly the second spray at the same site reduced growth less (Fig. 32).

The xylem growth in the year before spraying, i.e. 1965 in plantation one and 1967 in plantation two, was, by chance, not exactly the same in the trees selected for treatment as those in the controls (Figs. 31 and 32). Therefore, growth in the various treatments was compared relative to growth in the year before spraying (Table 13). This showed that the increasing effect of the spray on growth at the first plantation was clearly significant in all years after the first. The immediate reduction in growth resulting from the first spray at the second plantation was also statistically highly significant; even the lesser reduction in growth produced by the second spray could be substantiated statistically.

The 1967 and 1968 xylem growth of trees at the second plantation was measured in both October 1968 and November 1969; the same trees were sampled at the same height, but at different aspects of the bole, on each occasion. Neither the 1967 nor 1968 growth changed in width between the two sampling dates (Table 14); this showed that cambial growth was completed by October and that no compression of the xylem occurred.

Phloem growth was not affected by PMA. The phloem and cortex, produced in 1968 and observed on 17 October 1968 in trees at the second plantation, measured 1.96±.06 mm in the untreated trees and

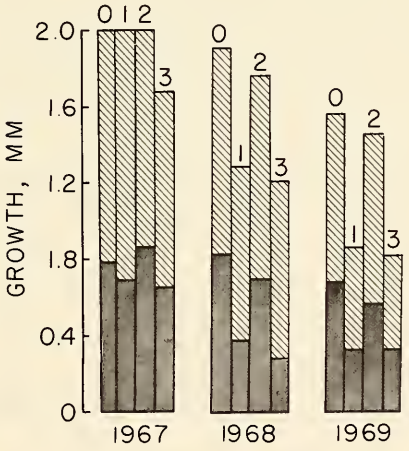

Fig. 32. Radial growth of the xylem at the second plantation for the 3 years prior to sampling in November 1969. Untreated (0) trees and trees treated with PMA on the first (1), second (2) and both (3) occasions in 1968. Hatching denotes spring growth and shading denotes summer growth.

Table 13. Xylem growth of the bole as a percentage of xylem growth the year before treatment. Measured from increment cores.

Year of Growth	First Plantation		Second Plantation			
	Treatment		Treatment			
	Untreated	Treated	None	First	Second	Both
1966	90± 5	80±4 n.s.				
1967	110± 9	63±4†				
1968	117±12	56±4†	96±3	66±4†	87±3°	81±7°
1969	114±13	48±4†	81±4	42±3†	67±4°	60±9°

° Significantly different from the untreated trees at the 5% level.
† Significantly different from the untreated trees at the 0.1% level.
n.s. Not significantly different from the untreated trees.

1.82±.08 mm, 1.84±.08 mm and 2.02±.10 mm in the trees sprayed on the first, second and both occasions, respectively. The measurement of phloem and cortex growth from previous years was difficult because of uneven compression of the dead tissue and secondary cambial activity.

The bole expansion measured by the dendrometer was consistently greater than the xylem growth measured from the increment cores in both sprayed and unsprayed trees. Avoiding 1966 since the dendrometer stations were not established until well into the growing season, we see that the bole expansion observed by the dendrometer in the untreated trees in the first plantation was 22% greater than the xylem growth in 1969 and 68% greater in 1968; the mean difference for both plantations over 3 years was 47%. The dendrometer, which measures growth between the heartwood (into which the nails were driven) and the brass ring of the dendrometer station, includes the growth of the phloem, cortex and bark. Since treatment with PMA did not restrict phloem growth, the difference between the bole expansion measured by the dendrometer and xylem growth measured from increment cores should be even greater in treated trees. This was indeed true: the bole expansion was 37% to 130% (with a mean of 72%) greater than xylem growth. The difference

Table 14. Comparison of the xylem growth (mm), measured from increment cores at the same height and from the same trees, in October 1968 and November 1969. Plantation two.

Date Sampled	Treatment			
	None	First	Second	Both
		A. 1967 Xylem		
Oct. 1968	1.93±.08	2.06±.14	1.95±.12	1.84±.15
Nov. 1969	2.02±.09	2.04±.14	2.04±.09	1.68±.18
		B. 1968 Xylem		
Oct. 1968	1.78±.09	1.28±.09	1.71±.12	1.15±.13
Nov. 1969	1.91±.09	1.29±.09	1.80±.11	1.21±.11

between the measured bole expansion and xylem growth was, however, smaller than the phloem growth measured from the increment cores in October 1968. This presumably arose from compaction of older phloem as new phloem was produced; as noted earlier, the xylem is not compressed.

Radial or cambial growth, which is often studied because of its economic importance, is only one measure of the total production of the tree; we also studied the growth of the internodes and needles. Extension of the internodes, which begins earlier than cambial growth, reaches a maximum in early- to mid-June and has ceased by mid-August (Kienholz, 1934), and it apparently uses stored carbohydrates rather than current assimilates (Larson, 1964). Needle growth, which begins about 2 weeks later, is more dependent on current photosynthesis (Larson, 1964).

During 1968 and 1969 we observed the internode and needle growth at both plantations. Ten trees at the first plantation and sixteen trees at the second plantation were sampled on three dates in 1968 and again in November 1969. A single branch per tree from the same whorl, in the fourth to sixth whorls from the top of the tree, was sampled on each date. The internode length for all years subsequent to 1964 in the first and subsequent to 1966 in the second plantation was measured on lateral branches. Further, the needles were removed, counted and the length and dry weight of 25 undamaged fascicles obtained.

The rapid growth of the leader is shown in Fig. 33. When the trees

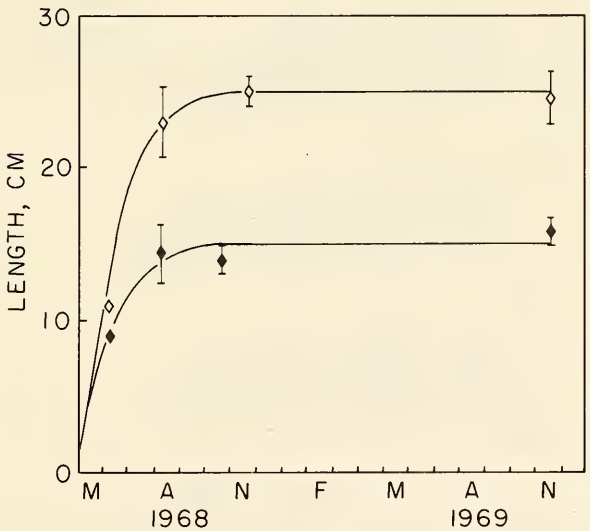

Fig. 33. Growth in length of the 1968 leader in 1968 and 1969 at the first (◆) and second (◇) plantations. Bars denote twice the standard error of the mean.

were sampled on 4 June 1968, the 1968 internode was still elongating; at that time its length was 10.1 cm (range 7.0 to 12.5 cm), but by the second sampling on 9 September 1968, the extension of the leader was complete and no further increase in length was observed in the subsequent year; this confirms previous observations in red pine in New England (Kienholz, 1934). Fig. 34 shows that the internode length tended to decrease in succeeding years, and extension growth of the pines at the second plantation was about 50% greater than in the trees at the first plantation.

A few measurements of internodes in 1967 revealed no effect of spraying with PMA. Similarly, PMA did not affect the internode growth in 1968, but a significant reduction was observed in 1969 (Table 15). This is some two years after we first observed a marked decline in bole expansion at the first plantation (Table 13). At the second plantation, radial growth was more quickly reduced by PMA (Fig. 30 and Table 13), and similarly the internode lengths were more quickly affected there by PMA (Table 15).

Needle lengths in our experimental plots are summarized in Fig. 35. The length of the fascicles increased in succeeding years, the converse of the observed decrease in internode length, Fig. 34. When first meas-

Table 15. Internode lengths as a percentage of the length in the year before treatments were applied. Standard errors are also given. The trees were sampled in the four months noted and the lengths are tabulated according to the year of growth.

Year of Growth	First Plantation		Second Plantation			
	Treatment		Treatment			
	Untreated	Treated	None	First	Second	Both
			A. June 1968			
1967	79± 4	77± 5				
1966	95± 4	111± 5				
			B. September 1968			
1968	59± 4	52± 5	85±7	86± 4	92±18	86± 1
1967	83± 8	75± 6				
1966	94± 6	116±14				
			C. November 1968			
1968	71± 6	76±28	87±3	89± 4	92± 6	83± 2
1967	90± 6	82±21				
1966	92±11	99±17				
			D. November 1969			
1969	68± 3	46± 5	94±5	71±11	63±17	73± 8
1968	60± 3	50± 4	83±2	85± 7	71± 8	79±13
1967	81± 4	78± 5				
1966	99± 4	101±10				

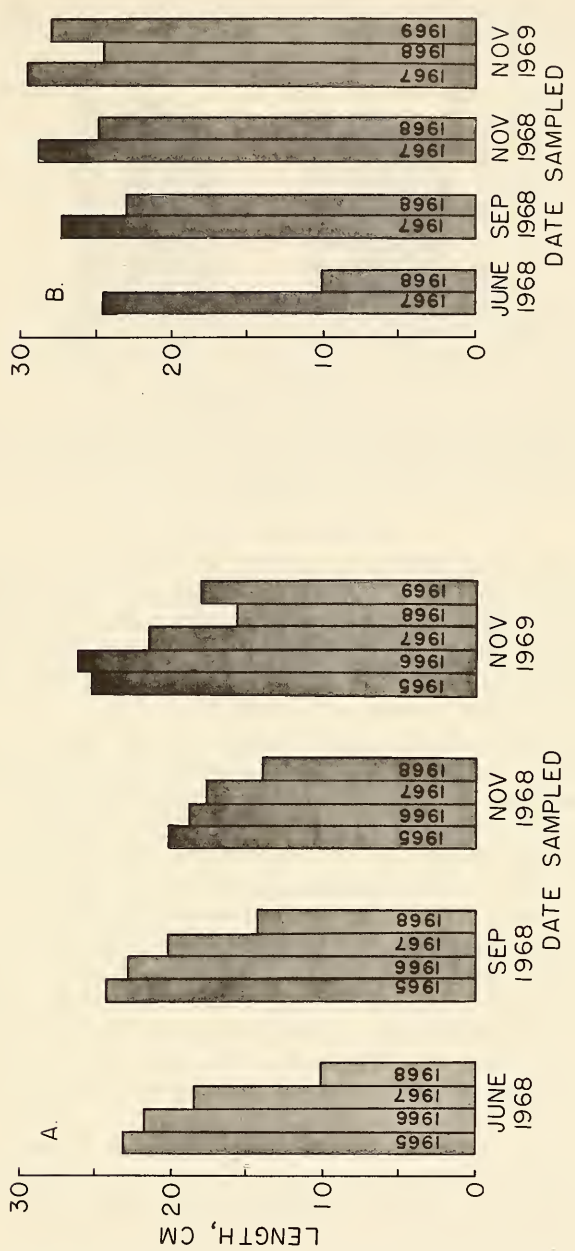

Fig. 34. Internode lengths of untreated branches on three dates in 1968 and November 1969. The year of origin of the internode is noted. Branches from the same whorl were sampled on each occasion: A, first plantation; B, second plantation.

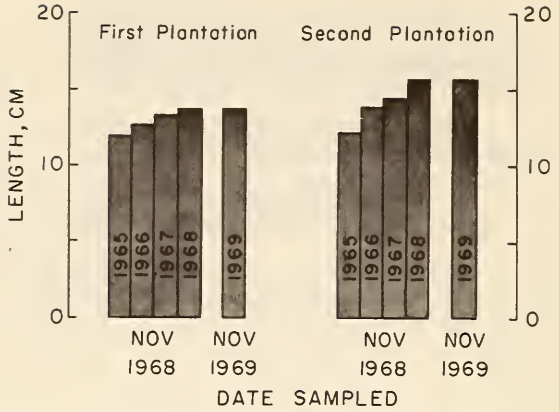

Fig. 35. Length of needles at the first and second plantations measured in November 1968 and November 1969. The year of origin of the needles is noted.

ured on 16 July, the 1968 needles were still growing. On that date the needle lengths were 10.9±0.4 cm on unsprayed and 10.0±0.1 cm on treated trees at the first plantation. Needle growth had ceased by September, and no difference in length was observed between September and November in needles of any age. PMA had no effect on needle length at any time.

In summary, the dendrometer revealed 1 to 1½ mm expansion of the xylem, phloem and bark in the boles during May through August in the first plantation and more in the second plantation. Cores taken from the boles showed that about two-thirds of this increment was xylem. Although this growth in the first plantation was scarcely affected by the first treatment with PMA, by the fourth year it was decreased to half. In the second plantation, where the first spray caused defoliation, the growth was promptly decreased. Extension of new internodes, on the other hand, was much less affected and extension of needles was not affected at all by PMA, making its total effect upon growth much less than its dramatic halving of xylem growth in the last year.

Thus, PMA has shrunken stomata and will, in the next chapter, allow us to test whether stomatal management can alter evaporation from a real forest. PMA, as we have seen, affects more than stomata; it reduces the surface area of foliage on the trees, and it can cause chlorosis, defoliation and decreased growth as observed in 1968. We must be careful not to confuse the effects of defoliation and damage on evaporation with the effect of stomatal shrinkage. Since treatment with PMA was omitted in 1969, a year with little foliage, we can separate this effect from that of stomatal closing on evaporation. Moreover the damage and poor growth encountered in the later years was not characteristic of the first year, which therefore gives us a measure of the effect of stomatal closure

alone on evaporation. Because foliar injury is a peculiarity of PMA, we can go on to examine the reduction of evaporation by stomatal closure, and use this as a measure of the saving of water that an ideal stomatal closer would achieve.

Chapter 8
THE SOIL WATER

The water contents of eleven 30-cm-deep strata of soil were measured, and they show the supply of water available to the roots, which supplied the water to the tree trunks and the transpiring foliage. The change in water content of each stratum showed which soil region was the favored source of water for the roots. Later these same observations of water content will be employed to estimate the evaporation from the forest. In this chapter, however, we only explain the method of measurement, show the water content, and explore the causes for extraction of water from one stratum rather than another.

The volumetric percentage of water in the soil was observed by the neutron scattering technique (see, for example, Van Bavel *et al.*, 1961), and the percentage was converted into the amount of water stored in the soil by multiplying by the depth of soil in the stratum. The change in storage was indicated by subtracting observations at, say, weekly intervals.

In the neutron scattering technique a source of fast neutrons is lowered into the otherwise undisturbed soil through an access tube. The neutrons are slowed by collisions with the hydrogen atoms in the soil, which are mostly in water molecules. Then a detector attached to the source reveals the number of slow neutrons produced by the collisions and hence the volumetric concentration of hydrogen atoms and water molecules. The instrument was a Model 105A neutron moisture meter manufactured by Troxler Electronic Laboratories, Raleigh, North Carolina. The source of neutrons was 50 or 100 mc of americium beryllium and the number of radiation events was counted for 30 or 60 seconds. Five to twenty thousand events were detected. The active center of the device was determined, and observations were made at 30, 60, . . ., 330 cm.

The variation in the observations, i.e. the proportion of radiation events counted or counts per minute (cpm), is caused by variation in the emission of neutrons, in the duration of the counting, in the position of the probe, and in the variation from place to place of water and other hydrogenous molecules in the soil. The variation in the water content from place to place is by far the greatest of these sources of variation (Hewlett *et al.*, 1964), making estimation of water content less precise than the estimation of the change in water content at a given place.

Thus, on 27 August 1969 the mean content in 36 sites at a depth of 90 cm was 6470 cpm with a standard error of 1174, whereas the change in content during the preceding 47 days was 1211 with a standard error of only 81.

The calibration of the probe in terms of water content is somewhat troublesome, mainly because the neutrons are scattered through a larger heterogeneous volume than the usual volume of a gravimetric sample. Hence, we employed the manufacturer's standard calibration of the probe in cadmium chloride (Van Bavel *et al.*, 1961), checked the function of the instrument at least daily by an observation in a shield of organic matter, and converted cpm to volumetric water content by a standard divisor. Nevertheless, we tested the standard calibration by comparing the cpm to the water content of a core removed as the access tube was inserted in the plantation soil and found these observations agreed with the standard calibration as well as might be expected in the variable soil (Fig. 36). The observed calibration was somewhat above the standard. The slope of the observed calibration, however,

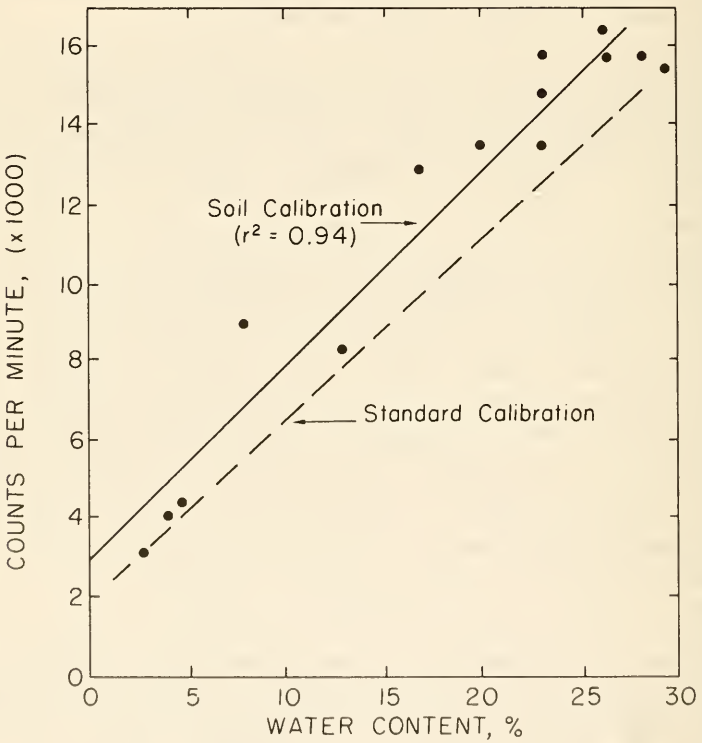

Fig. 36. The relation between volumetric water content and counts per minute by the neutron moisture meter in the plantation soil. The dashed line is the standard calibration obtained by submerging the probe in cadmium chloride solutions.

was insignificantly different from the standard. Because of the uncertainty of calibration with small samples of soil and because the slope alone is used in the critical estimates of *change* in soil water, the standard calibration was used.

The arrangement of the rectangular plots of the first plantation was described in Chapter 2. The 16 plots generally extended down a gradual slope and then a short distance up a somewhat steeper slope. At the highest location in each plot, a tube was inserted 360 cm into the soil, and at the lowest, another was inserted to the same depth. Four other tubes were inserted to a depth of 210 cm in each plot. Each tube was located about a half meter from a sound tree surrounded by other sound trees; the former were the trees on which the dendrometer stations were established and the needle fall trapped. Thus in the 16 plots, 96 observations of soil moisture were made at 30 cm, 96 at 60 cm, . . ., 96 at 180 cm, 32 at 210 cm, . . ., and 32 at 330 cm. As reported earlier, in the final two years a fourth of the plots were abandoned. This completes the description of the mechanics of observation, and we turn now to the observations of soil moisture beneath the untreated trees during four seasons.

Observations, as in Table 16, were taken on the occasions identified by the small arrows beneath the depictions of each year in Fig. 37. The water content on intervening days was interpolated linearly. The spots in Fig. 37 were darkened by multiple printing as the soil became wetter. Thus in the fourth stratum, 120 cm deep, the water content on 1 June 1967 was 24% (Table 16) and is heavily overprinted, whereas by 25 October 1967 the water content was only 16% and is not as heavily overprinted.

Several features of soil water use and distribution are apparent. The drought of the summer of 1966 (Chapter 2) caused a deepening depletion of water, which was then somewhat recovered in the upper layers by September rains. The alternate wet and dry months of 1967 caused wetting and drying of the upper strata, while the drying of lower strata proceeded much as in 1966. The protracted dry spell beginning in July 1968 dried the soil downwards in a regular pattern. Finally the drought of June 1969 caused the upper soil to dry, but since observations were not taken soon after the July rains, an extended drought was interpolated for the upper soil.

The usual pattern of first depletion of water from upper layers, despite roots extending to fully 2 meters (Table 1), is clearly evident in Fig. 37. The soil at 330 cm remained very moist. On the other hand, the sandy strata just above the lowest strata dried during September and October, while the finer-textured soil of the seventh stratum remained relatively moist; this behavior is as likely caused by the exchange—or lack of exchange—between strata of soil as by extraction by roots.

The great number of observations available provide an excellent opportunity for testing hypotheses about factors affecting loss of water

Table 16. Volumetric water content as a percentage at 11 depths beneath untreated pines in 1967. Rainfall between days of observation is also tabulated.

Depth cm	Date															
	Jun				Jul				Aug				Sep		Oct	
	1	8	15	28	5	12	19	26	2	10	16	23	6	13	25	
30	17	13	10	16	21	16	16	15	19	18	16	12	9	9	17	
60	18	15	13	15	19	16	16	14	15	16	15	13	10	9	16	
90	20	21	16	15	17	16	16	16	15	16	15	14	13	12	16	
120	24	22	20	18	19	19	19	18	18	18	18	17	15	15	16	
150	26	24	22	20	19	19	19	19	18	18	18	17	16	15	15	
180	26	25	23	21	20	20	20	20	20	19	19	18	17	16	16	
210	32	31	30	29	28	28	28	27	27	26	26	26	24	24	23	
240	29	29	28	26	26	25	25	25	25	24	24	24	23	23	21	
270	27	28	27	26	26	25	25	25	25	25	24	24	22	22	20	
300	25	26	26	25	24	24	24	24	24	23	23	23	21	21	19	
330	29	30	30	29	29	29	29	29	28	28	28	28	26	26	24	
Rain, mm	0	7	58	34	49	33	10	38	17	9	2	20	4	126		
Group		L	G	G	L	G		G	L	LL	LL	LL	LL			

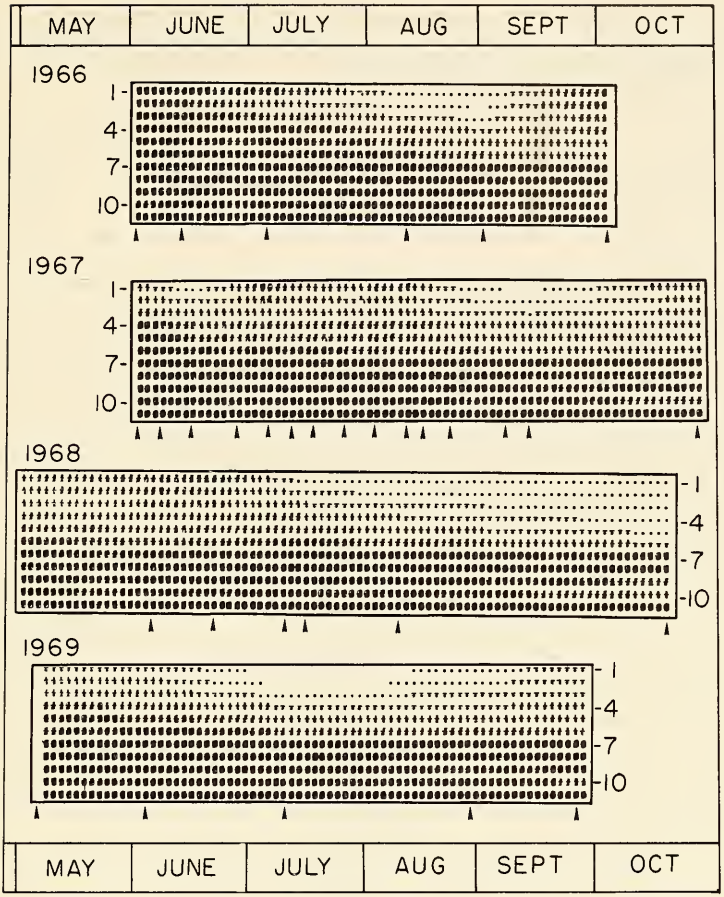

Fig. 37. The water in 11 soil strata measured by neutron probe at the times indicated by the short arrows beneath the panels depicting the 4 years. First plantation. The overprinting was increased with increasing moisture. (Program by T. Siccama, Yale Forestry School.)

from different strata. We are not, however, examining a controlled experiment with a few, great forces at work; therefore, correlation will be our tool, and only the simplest and clearest hypotheses should be examined.

The simple hypothesis examined is that the loss of water from the volume of soil examined by the probe, a sphere about 30 cm across, is a function of the loss P from the volume during the period just past, the amount of water I in the volume at the beginning of the present period, the amount of water B above the volume, and the depth Z of the volume below the soil surface. The rationale for the effect of past loss, P, is that a large past loss may indicate that many active roots

Table 17. The correlation coefficients among four independent variables: P, the past loss; I, the amount of water in the 30 cm spherical volume; B, the amount of water above the volume; and Z, the depth of the volume below the soil surface. From 1152 observations of group LL in Table 16.

	I	B	Z
P, past loss	−0.07	−0.42	−0.48
I, water in volume		0.28	0.25
B, water above			0.94

occupy the volume. Since the available moisture-holding capacity does not vary greatly (Table 1), ample water I in the volume allows ample loss. Since lower roots extract water more rapidly after upper ones have depleted their supply (Hunter and Kelley, 1946), sparse water B above the volume should increase the loss from the volume. Finally the rationale for the depth Z is that more roots are found near the surface, and thus more water should be lost there. Z was taken in strata of 30 cm, i.e. 1, 2, . . ., 6, and the lower depths were omitted because fewer observations were made there.

The 1967 observations provide the most numerous data. They were divided into three groups, which are identified at the bottom of Table 16. The group L occurred in the earlier part of the season, and they are three periods of loss of soil water. Two out of three periods were preceded by gains. The G group are the four periods of gain. Finally the four periods LL are later periods of loss, all preceded by losses. In all periods the loss in cpm, either positive when moisture decreased or negative when it increased, was standardized to a loss per day. To eliminate the effect of the weather, which is not under study in this section, the mean loss for all depths for the period was subtracted; for example, if the mean loss for a period was 100 cpm per day and the water in a particular soil volume decreased 90 cpm per day, the dependent variable or loss was −10 cpm per day for that particular soil volume.

Observations from 1968 were also examined. The periods of 20 June to 9 July, 9 to 15 July, and 15 July to 8 August are called L68 because they were times of loss preceded by losses. A fourth period, 8 August to 17 October, was examined separately.

The correlations among the four *independent* variables are shown in Table 17 for four periods of loss preceded by losses (LL, Table 16). The correlation between B and Z is obvious: the deeper the volume, the more the water above. The table also shows that the deeper the volume —and the more the water above—the greater is the amount of water I in the volume. Finally, the deeper the volume, the smaller is the past loss P.

To segregate the independent effects of P, I, B and Z upon losses of water from the soil, we employed a multiple regression analysis. The standard partial regression coefficients in Table 18 are designed to show the relative potency of the four independent factors upon the dependent variable, water loss. Being "partial" they show, for example, the effect

Table 18. Standard partial regression coefficients of the loss of water from a volume of soil on four independent variables: P, I, B, Z.

Group	Number of observations	Independent variables P	I	B	Z
G67	1152	0.30	0.10	−0.43	1.13
L67	864	−0.46	0.03	−0.22	−0.06
LL67	1152	0.12	0.24	−0.14	−0.41
L68	648	−0.04	0.13	−0.08	−0.58

of P independent of I, B and Z. Being "standard," they permit the comparison of the effectiveness of, say, B with Z although B has a standard deviation of over 10 thousand while Z varies from only 1 to 6. The coefficients of Table 18 are, of course, dimensionless.

The first line of the Table pertains to periods when moisture near the soil surface was increased more by rain than it was depleted by evaporation. The 0.30 coefficient indicates that volumes that had lost considerable moisture P in the past, indicating a zone of active roots, continued to lose water at a fast rate. However, the water content I had little effect under the conditions of a gain in water. As expected, the strata of soil with little water B above lost more water than those with plenty of water above them. Finally, the positive relation between depth Z and loss indicates that shallow volumes *gained* water.

During periods of loss in spring and summer, L67 (L, Table 16), the volumes of soil that had gained more water also lost more as shown by the −0.46 relating P to loss. Further the shallow depths did not gain more, as might be expected under these conditions.

The third and fourth lines in Table 18 represent periods of decreasing soil moisture within longer periods of drying. Clearly, past loss P and the amount of water B above matter little at these times, while the loss is greater at shallow depths. Finally, during late 1967 the soil moisture I in a volume began to limit the loss, as shown by the coefficient 0.24.

The seasonal change in the influence of I caused us to examine the change during 1968 of the simple correlations between loss and P, I and B for single periods of observation throughout a season in which the soil water progressively declined (Table 19). Because B and Z are closely correlated, Z was not considered separately but unquestionably is confounded with B.

During the early summer, water is lost more rapidly from those volumes in which prior losses P were greater, but this correlation is lost with declining soil moisture. On the other hand, the correlation between loss and the water content I in a volume grows as the soil becomes drier during the late summer and early autumn. Finally, the relation between B (or Z) and loss changes direction; i.e. in the early season greater losses occur from the shallower volumes with little water above them, while in the later periods the greater losses occur from the deeper volumes with more water above them.

Thus, the hypothetical relations between loss and the four independ-

Table 19. The seasonal course of the correlations between 216 observations of change of moisture in volumes of soil and three dependent variables—P, I, and B—and the mean water content, 1968.

Variable	Period 20 Jun-9 Jul	9 Jul-15 Jul	15 Jul-8 Aug	8 Aug-17 Oct
P	0.50	0.61	−0.31	0.19
I	0.05	−0.24	0.46	0.66
B	−0.79	−0.61	0.24	0.60
Mean water content, % v/v	20	17	16	14

ent variables depended upon whether the soil was gaining or losing water and whether it was wet or dry. Losses were greater where past losses were greater if the soil was moist but not recently moistened. Losses were greater where moisture was greater if the soil was dry. The moisture above a volume had rather little effect, but depth had much, with shallow volumes losing much water when the entire soil profile was moist and deep volumes losing more when the profile was drier.

We shall see in the next chapter that PMA reduced the evaporation from the forest. Logically, and in fact, this increased the amount of water in the soil under the treated trees; the increases were small, however, compared with the total water in the soil. Since it is more meaningful to discuss the effect of PMA on evaporation, rather than on soil water content, we shall defer our discussion of PMA and soil water, and first explain the use of our observations of soil water to calculate evaporation.

Chapter 9

EVAPORATION FROM THE FOREST

Evaporation is, in a sense, the culminating subject that the preceding chapters lead to. It will be estimated from the soil moisture observations described in Chapter 8 and from rainfall observations. These estimates will be presented after a theoretical framework is given for the effects of weather and foliar area and stomata upon evaporation.

Weather is surely the predominant controller of the evaporation from a heavy and moist canopy of leaves. Thus, Thornthwaite (1948) and Penman (1956) were able to estimate "potential" evaporation from the weather alone, neglecting the complications of differences among plants. We shall examine the effect of weather upon evaporation from the Voluntown pines, both theoretically and by observation.

Beneath the maximum set by potential evaporation, however, there is scope for significant differences in evaporation caused by differences

among plants. Some of the differences were incorporated into the Penman (1956) equation: it has a place for altered reflectivity and roughness. Thus a dark, rough forest was expected to have a rapid potential evaporation; in fact, Penman (1967) calculated that conifers on a lysimeter in Castricum, Holland evaporated fully an eighth more than potential transpiration from a very dark stand of plants. The Penman (1956) equation even included a term for an average stomatal resistance for the entire canopy, but there was as yet no explicit rule for how the stomatal resistances in the several levels of the canopy would be combined with foliar area to produce the average resistance.

Experiments by foresters, who cut and pruned trees, showed that severe changes in leaf area would increase the flow of water downstream (e.g. Hewlett & Hibbert, 1961; Lull & Reinhart, 1967), but many questioned whether smaller differences—as between broad-leaved and conifer trees—would affect evaporation and hence the yield of water to streams.

Chemicals that would shrink stomata without general toxicity to foliage were discovered by both Ventura (1954) and Zelitch (1961). These proved powerful tools in revealing any role of stomata as well as any effect of small differences between plants in the control of evaporation. Thus, decreases in evaporation through partial stomatal closure were soon produced in several cases of individual leaves or plants standing alone, as reviewed in Chapter 1. Eventually, evaporation from a barley crop was decreased by stomatal closure (Waggoner *et al.*, 1964). When an entire watershed covered by a hardwood forest was sprayed from the air with a stomata-closing chemical, however, the stomata on the undersides of the leaves were not reached by the spray and the experiment failed (Waggoner and Hewlett, 1965).

Thus two tasks remained: to develop a model of energy exchange and evaporation within a canopy that will logically relate foliar area and stomatal resistance to evaporation, and to show experimentally whether doubling the resistance of the microscopic stomata as in Fig. 8 will significantly change evaporation and thus the hydrologic cycle. During the years of the Voluntown experiment these tasks were accomplished and have been partially reported; the model is reported briefly here as a guide to the experimental results, and then the results are fully reported.

The essence of the model or simulator of energy exchange (Waggoner and Reifsnyder, 1968; Waggoner *et al.*, 1969b) is shown in Fig. 38. A forest is divided into (n-1) strata of foliage and a lowest stratum of stems and soil surface. In the Figure, n is 4. Each stratum absorbs a net S_i calories per second of radiation per cm^2 of land. The subscript i identifies the stratum and may be 1, 2, . . ., n. At steady state the foliage attains a temperature of θ_i that causes a loss of h_i sensible heat and v_i potential heat or evaporation that balances the gain S_i. At the soil surface, the current of energy G into the soil helps balance the budget. The loss of sensible heat h_i is determined by the θ_i, the temperatures T_a at the top of the canopy and T_s near the soil, the boundary layer

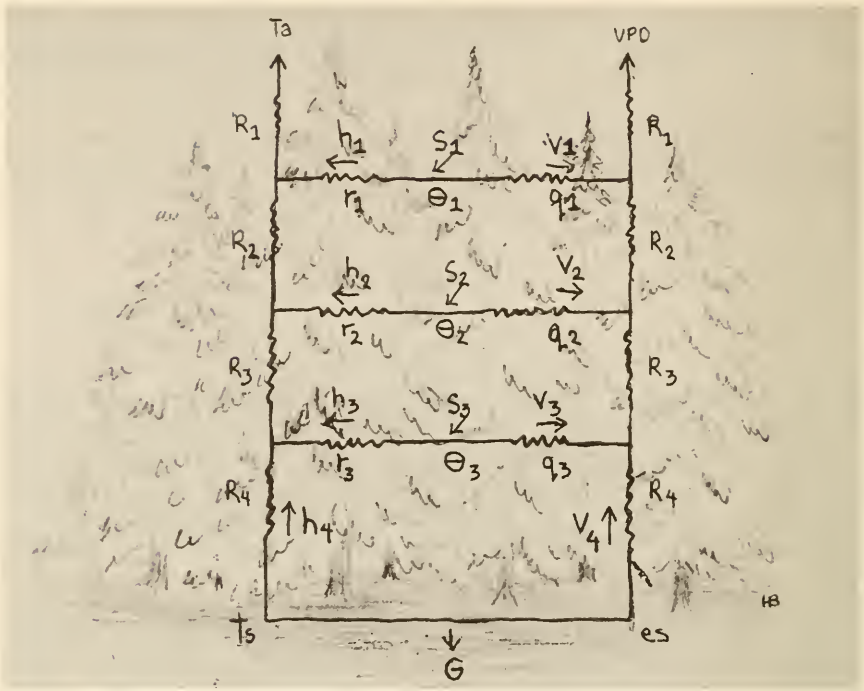

Fig. 38. The conception of energy exchange in a forest (see text).

resistances r_i, and the resistances R_i of the bulk air. The evaporation v_i is determined by the θ_i (under the assumption that the vapor pressure is saturated beneath the stomata), the humidities VPD and e_s at the top of the canopy and near the soil, the R_i, and the q_i. The q_i is the sum of r_i and stomatal resistance. Since all differences in temperature or humidity are proportional to the products of resistances and either h_i or v_i, linear equations can be written. These equations plus the balance of energy in each stratum comprise 3n equations that can be solved for n evaporation currents as well as n currents of sensible heat, (n—1) foliage temperatures, and G.

A modification of the algebra permits specifying G, v_n and h_n, the flux of heat into the soil and the fluxes of evaporation and sensible heat from the soil, instead of T_s and e_s. Since conceiving the currents G, v_n and h_n for a hypothetical day is easier than conceiving T_s and e_s, this modification is employed here.

Evaporation is now calculated for a forest with the following characteristics. The temperature, humidity, net radiation, wind and diffusivity at canopy top are tabulated in Table 20 for a hypothetical but realistic clear day. The flux of heat into the litter-covered soil was taken from Schubert's observations in a pine woodland (Baumgartner, 1965).

Table 20. Weather at the top of the simulated pine forest and heating of the soil: a hypothetical clear day.

Hour	Temperature, C	Vapor pressure deficit, mm Hg	Net radiation, mly sec^{-1}	Wind, cm sec^{-1}	Diffusivity (X1000), cm^2 sec^{-1}	Heat into soil, mly sec^{-1}
0	20	2	−1	100	2	0.4
2	20	0	−1	100	2	0.4
4	19	0	−1	100	2	0.3
6	19	4	−1	100	2	0
8	23	8	11	150	10	0.6
10	26	12	15	200	16	1.0
12	27	14	16	300	20	1.0
14	27	14	15	300	20	0.8
16	25	11	11	300	16	0.4
18	22	4	−1	200	4	0.3
20	20	2	−2	100	2	0.5
22	18	2	−2	100	2	0.5

Evaporation and condensation at the soil surface were assumed to be negligible. A cloudy day was simulated by quartering radiation, flux of heat into the soil and daytime warming of the air, and by halving the vapor pressure deficits of Table 20.

In June 1969 the trees were 1540 cm tall, the live canopy 810 cm tall and the needles 1.4 mm wide. The projected leaf area was 2.6 cm^2 cm^{-2} and the leaf surface area was 12.4 cm^2 cm^{-2} (Chapter 3). To simulate defoliation by treatment in 1968, the outcome of a loss of a third of the foliage was also calculated. The foliage was distributed vertically as the Gaussian curve (Stephens, 1969).

The wind and diffusivity were extinguished exponentially through the canopy as a function of relative height and an extinction coefficient (Uchijima, 1962). In other canopies the coefficient has ranged from 2.5 in clover to 4.2 in 10-year-old pine (Brown and Covey, 1966). Because the open space among the stems at Voluntown was great and foliage area was small, a coefficient of 3, i.e. a decrease to 5 per cent through the canopy, was assumed. Further, the diffusivity throughout the stem stratum was set equal to that in the lowest canopy stratum, and a minimum of 244 cm^2 sec^{-1} was established.

The illumination was extinguished exponentially with the projected foliage area (Saeki, 1963) and an extinction coefficient of 0.6, which causes only slightly more absorption of illumination than our observation (Chapter 3) of 70 per cent absorption of illumination in a leaf area of 2.6. A somewhat smaller coefficient, 0.5, was employed for the extinction of net radiation.

Since stomatal resistance r_s varies with illumination, it was calculated as

$$r_s = r_m \,/\, \mathrm{erf}\ (I/C) \qquad (5)$$

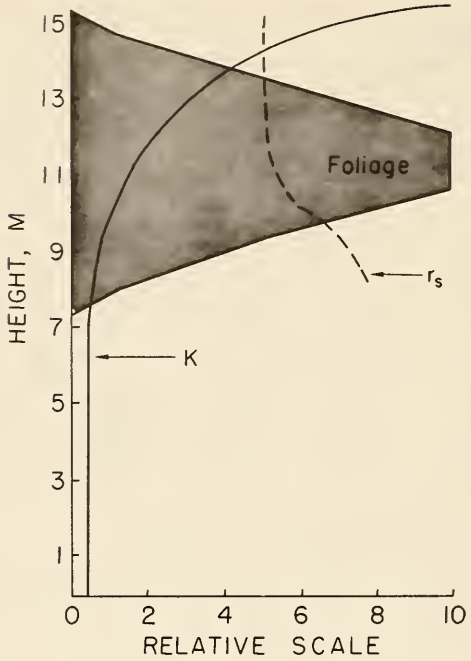

Fig. 39. The midday distribution, in relative terms, of stomatal resistance (r_s), diffusivity (K) and foliage through the simulated pine.

where r_m is a minimum stomatal resistance of 15 sec cm^{-1} (Figs. 6 and 10), I is insolation absorbed per projected foliage area, C is 0.005, and erf is the error function. The insolation at canopy top was taken as 1.54 times net radiation. The C of 0.005 fits the observations of stomatal resistance and insolation, Fig. 10A. The r_m was taken as 30 in treated foliage, Fig. 8A; an r_m of 7.5 represented newly formed foliage, Fig. 7; and an r_m of zero represented wet foliage. Since the stomatal resistances above pertain to each square centimeter of leaf surface (Equation 4), the foliar surface area, and not projected area, per stratum was used to obtain the r_l of Fig. 38.

The distributions or profiles of the foliage, diffusivity and stomatal resistance are exemplified in Fig. 39. The profile of stomatal resistance is similar to those observed by Turner (1969), and its unusual shape arises from the non-linearity between resistance and light (Equation 5); the resistance profile in Fig. 39 is for midday.

The outcome of different stomatal resistances at 1200 hr on a clear day is shown by the partitioning of energy between evaporation and sensible heat, Fig. 40, and by the accompanying temperatures of foliage and air, Fig. 41. In Fig. 40 seven pairs of horizontal bars show the exchange of energy in each of the six canopy strata and at the soil. The upper one of each pair shows the outcome when the minimum stomatal

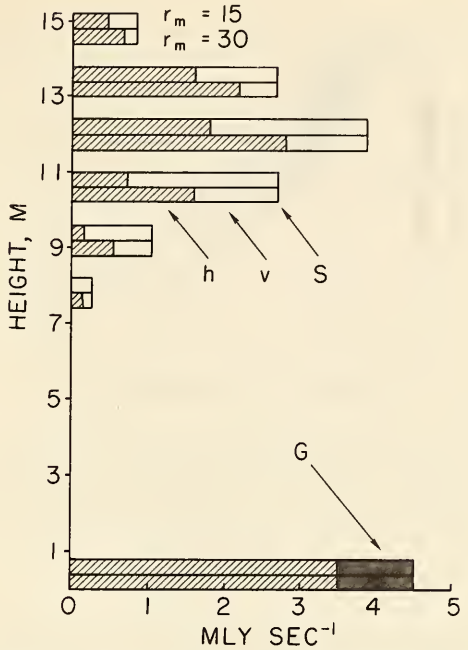

Fig. 40. The midday partition of the gain of radiation (S) into sensible heat (h), evaporation (v) and the ground (G) when the minimum stomatal resistance (r_m) is 15 or 30 sec cm^{-1}.

resistance is 15 sec cm^{-1}, and the lower shows the outcome when it is 30 sec cm^{-1}.

The net income or gain of radiation is indicated by the lengths of the bars at each level or stratum. The sum of the six S_i in the canopy is 11.5 mly sec^{-1}, leaving 4.5 to be absorbed by the soil. The 4.5 is divided between 1.0 into the ground and 3.5 sensible heat into the air. The sensible heat h is indicated in the Figure by hatching and the ground flux G by shading. This division at the soil is the same for both stomatal conditions because ground flux was specified and S was calculated from the constant foliar area.

Within the canopy, however, stomatal conditions matter. Essentially, increasing stomatal resistance decreases evaporation v and increases the loss of sensible heat h, and in Fig. 40 this is shown by an increase in the hatched bars for an r_m of 30 compared to 15 sec cm^{-1}.

The greater loss of sensible heat when stomatal resistance increases, of course, is accompanied by a warming of foliage relative to air and a warming of the air within the canopy relative to the air above. These changes are depicted for midday in Fig. 41. Relative to air above, the air within the canopy is 0.26C warmer in the highest and 3.90C warmer in the lowest stratum when r_m is 15 sec cm^{-1}. Doubling r_m warms the

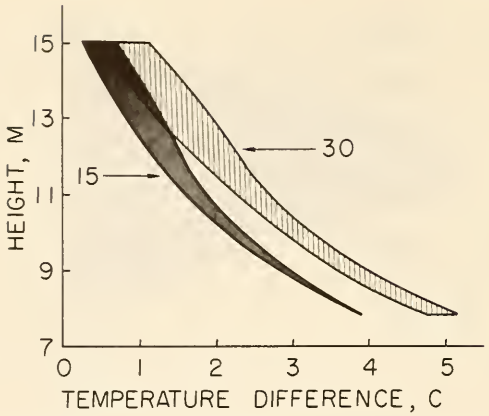

Fig. 41. Midday air temperature within canopies having an r_m of 15 and 30 sec cm^{-1}. The line at the left of each shaded portion is the air temperature, relative to the air temperature at the canopy top. The width of the shaded areas is proportional (2×) to the warming of the foliage above local air temperature and, at a given height, is proportional to the loss of sensible heat (h).

air 0.09C in the highest and 0.79C in the lowest stratum. At the same time, the difference between foliage and local air temperature increases from a maximum of 0.13 to 0.17C in the second stratum, and this is depicted by a widening of the shaded areas in Fig. 41.

If stomatal resistance is halved, as in new foliage, the outcome is, of course, reversed. Evaporation is increased by 30 to 100 per cent in the several strata. In the bottom half of the canopy, this rapid evaporation consumes more energy than radiation provides, the foliage becomes cooler than the nearby air, and the needed energy is gained as sensible heat. If the foliage were wet, as after a rain or dew, the foliage would become still cooler, still more energy would be gained as sensible heat, and evaporation from the whole canopy would exceed the receipt of net radiation.

Clearly, midday, which was considered until now, is the time of greatest effect of stomatal change. To show the outcome of changed weather or foliar area or stomata upon soil moisture, however, we must add the evaporation v_l over height and over the day. The effect of halving or doubling minimum stomatal resistance r_m in the full canopy of 2.6 cm^2 cm^{-2} is shown in the course of evaporation during a clear 24 hours, Fig. 42. During daylight the differences among minimum stomatal resistances affect evaporation. At night, however, real and simulated, treated and untreated, old and young stomata all close; then the differences among minimum stomatal resistances do not affect evaporation.

At this point, we interject a comment about the outcome of zero stomatal resistance because one wants to know how rapidly dew or in-

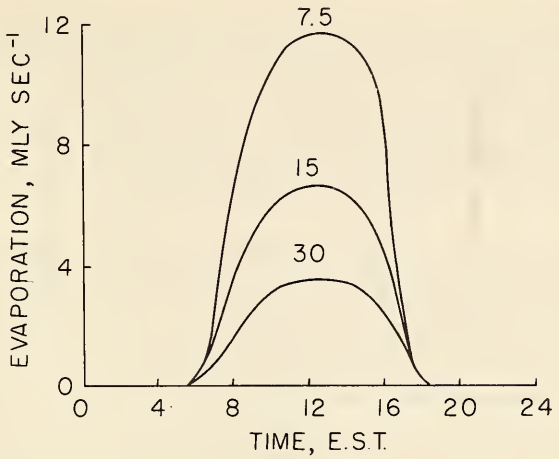

Fig. 42. The diurnal course of simulated evaporation from a pine plantation with minimum stomatal resistances of 7.5, 15 and 30 sec cm.$^{-1}$.

tercepted rain would evaporate. This evaporation of water on the foliage ranges from 1 mm hr^{-1} (100 mly sec^{-1}) at 0800 hours on a cloudy day to 4.8 on a clear midday, providing an ample route for the prompt departure of any dew or intercepted rainfall and explaining how the evaporation of intercepted precipitation may be a third of the evaporation from a forest (Baumgartner, 1967).

It is now time to summarize the various evaporations by setting out in Table 21 the total quantities lost in 24 hours. A canopy of young foliage on a clear day would transpire 5.8 mm of water, consuming about 85 per cent of the net radiation. Any evaporation from the soil surface would be added to this as would much of the evaporation of any intercepted water. Cloudy weather, as defined here, would decrease the daily evaporation to about a fourth, which is about the same as the specified change in net radiation. Doubling stomatal resistance would decrease evaporation about 45 per cent, whether one begins with an r_m of 7.5 or 15 sec cm^{-1} and whether the weather is clear or cloudy.

Table 21. Simulated daily evaporation (mm).

Projected Leaf Area	2.6			1.7		
Minimum stomatal resistance, sec cm^{-1}	7.5	15	30	7.5	15	30
Clear day[a]	5.8	3.3	1.8	4.6	2.6	1.4
Cloudy day[b]	1.2	0.7	0.4	1.0	0.5	0.3

[a] As specified in Table 20. Net radiation was equivalent to 7 mm evaporation.
[b] One quarter the net radiation and soil heat flux and one half the vapor pressure deficit of the clear day. Otherwise the same as the clear day.

The final calculation concerns the effect of the one-third decrease in foliage that was apparent by late 1968 and caused by repeated spraying. According to Table 21 this defoliation would decrease daily evaporation about a fifth under both cloudy and clear conditions.

We now have a logical framework and predictions for the effects of several factors upon evaporation and can analyze the changes in evaporation that will be derived from soil and rain observations.

Evaporation from the forest was calculated as the sum of the loss in water in the top 330 cm of soil plus the rainfall. These two parameters are tabulated in Tables 22-24. The estimate of evaporation will be high if considerable water leaches below 330 cm and will be affected by the variability in soil water content and rainfall. The error due to leaching is unknown. The variability caused by soil water content differed from one period to another, but an example is provided by the change from 1 to 7 June 1967: there was a 44.1 mm change in the upper six strata with a standard error of 1.3 mm, and 6.0±2.9 change in the lower five strata. The variability due to rain was reduced but not eliminated by using rainfall observations made at the Pachaug State Forest Nursery 3 km away rather than those made at the Pachaug State Forest Headquarters 5 km away (Table 2).

During the four years of observation, loss could be estimated from 28 pairs of observations representing 28 periods of 6 to 70 days, and the mean rates for each period are shown in Fig. 43. They range from 7 mm day^{-1} during eight bright days in June to about 2.5 mm day^{-1} in the autumn or during eight cloudy days in August 1967. The smooth curve in the Figure is the best-fitting, two-term polynomial. It is a reasonable estimate of the climatic normal, since it was calculated from four years of observations. The mean evaporation from the pan at Kingston (Table 3) is also shown on the Figure, and it is essentially the same as the estimated mean evaporation from the forest.

Next, the causes of the variations about the mean curve were explored. The evaporation from the pan is an integration of factors that differ between clear and cloudy days, and hence the evaporation from the forest per day during a period was related to the daily loss from the pan during the same period. The method of presenting the relation between loss of water and evaporation can greatly affect the appearance of the correlation. Sometimes evaporation from a field is accumulated over a season and compared in a graph to an estimate of the evaporation, in this case the accumulated evaporation from a pan. Since both values inevitably increase through the season, one sees an illusory correlation of observation and estimate. A more critical test is to compare the evaporation *per day* from the plantation and pan. This method exposes the difficulties in a glaring light, but it is nevertheless the test used in Fig. 44.

The few observations of 1966 and the more numerous ones of 1967 show the significant effect of the evaporation from the Kingston pan

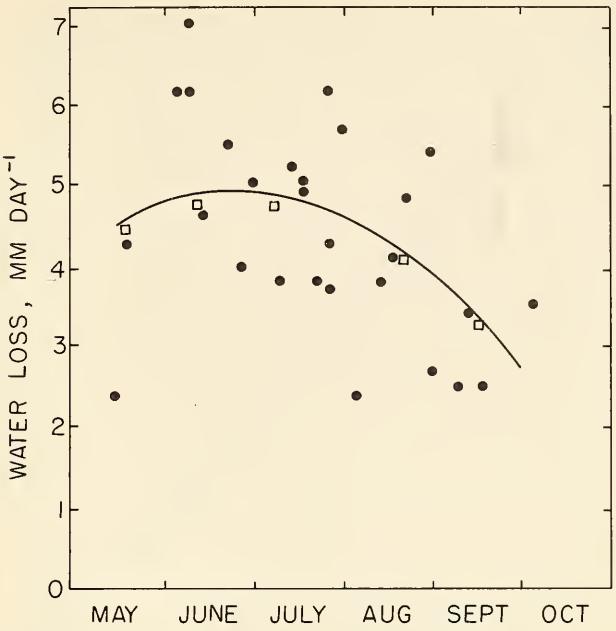

Fig. 43. The course of water lost from untreated trees at the first plantation during the four seasons (●) and the mean pan evaporation at Kingston (□).

upon the loss of water from the forest. One adjustment was necessary before the correlation coefficients of 0.73 in 1966 and 0.55 in 1967 were obtained: the 5 July 1967 observation was made during a 3-day rain, and hence, the evaporation was better estimated for the 2-week period including 5 July than for the week before and after 5 July. The correlations show the sort of difference between relatively clear and cloudy periods that we expect, but the correlation is not close.

A comparison of the insolation at the Pachaug State Forest Nursery, 3 km from the plantation, and pan evaporation at Kingston, 30 km from the plantation, shows that occasionally cloudiness or persistent fog at Pachaug reduced the daily insolation, while clear skies at Kingston caused rapid evaporation, and vice-versa. Since evaporation is logically related to net radiation (Penman, 1956), which varies with and is about 0.8 of insolation (Shaw, 1956), and since this is also true when other weather factors vary accordingly (Table 21), we tested whether the water loss from the plantation was more closely related to insolation at the nearby Nursery than to the pan evaporation at further Kingston. The relation between insolation, converted into equivalent evaporation by dividing by 60 cal mm^{-1}, is shown in Fig. 45. The closer correlation ($r = 0.73$) between insolation upon the Nursery and water loss in 1967 than the correlation ($r = 0.55$) between Kingston evaporation and water loss (Fig. 44B) indicates that some deviation was caused by the distance

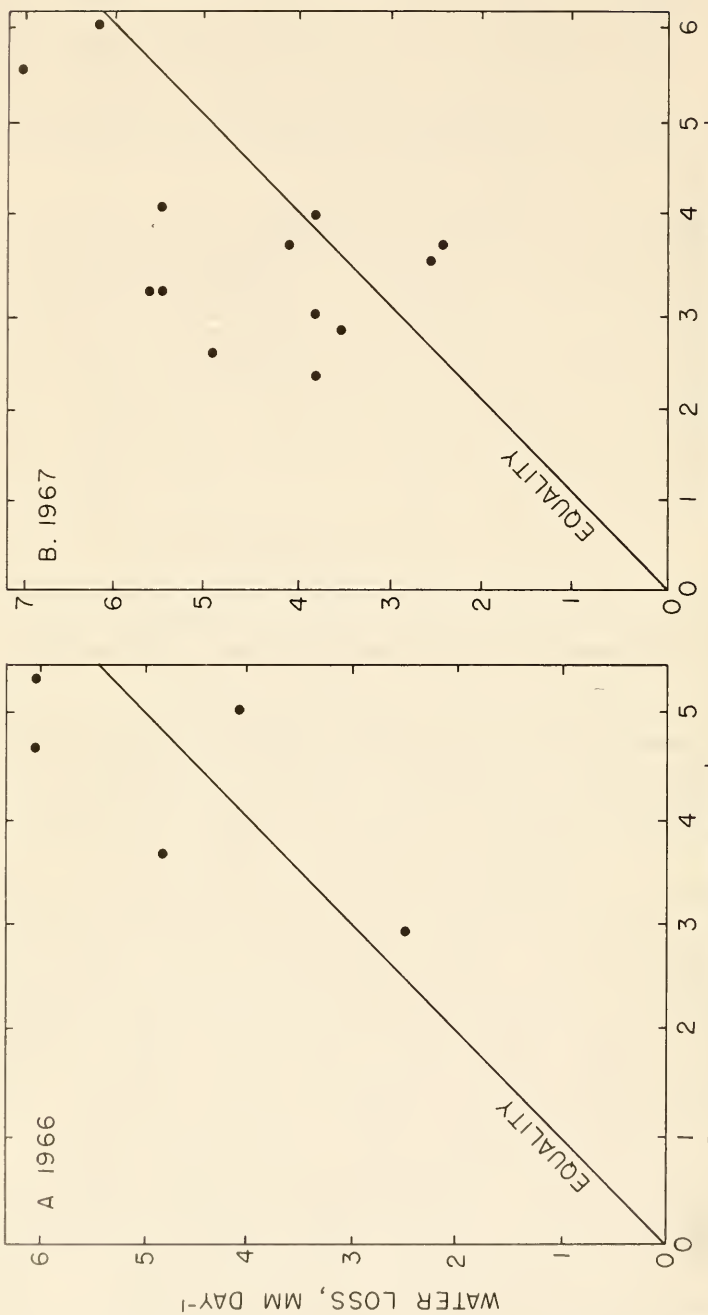

Fig. 44. Loss of water from the first plantation related to evaporation from a pan at Kingston. A, 1966; B, 1967.

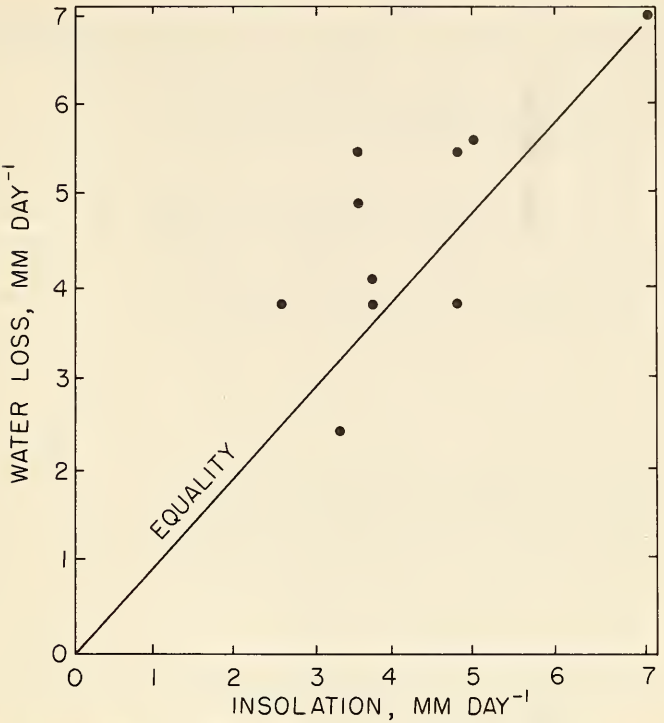

Fig. 45. 1967 loss of water from the first plantation related to insolation upon the Pachaug State Forest Nursery.

between the plantation and observatory and that water loss is indeed closely related to evaporative demand. Thus, if one accepts that the loss of water from the forest should logically vary with either the evaporation from an open pan or the radiant energy, then the *correlations* of the three Figures are recommendations for our system of estimating the evaporation from the forest.

The *equality* of evaporation from the forest and either pan evaporation or insolation, however, is another matter because Table 21 shows that theoretically evaporation would be less than net radiation (which was 7 mm day^{-1} in the example). Three causes for the rapid rates estimated for the forest can be suggested. First, slow leaching beyond the deepest soil observation and slow evaporation from the soil both undoubtedly occur and would have to be added to the estimates of Table 21. Second, the forest reflects little radiation and the net radiation receipt is likely a larger fraction of the insolation than the ratio of 0.8 observed over grass by Shaw (1956). Third, rain fell during many of the periods and the intercepted rain plus any dew distilled from the soil depart rapidly as we have calculated earlier and also observed (Waggoner *et al.*, 1969a).

Thus our estimates of evaporation are rapid partly because of the downward escape of water, but they must also be taken as confirmation of the rapid evaporation from conifers already observed at Castricum (Penman, 1967) and in England (Rutter and Fourt, 1965).

The savings in evaporation caused by treatment, Tables 22-24, were calculated by subtracting the change in soil water beneath treated trees from the change beneath untreated trees. The greater changes, savings and number of samples were in the upper six strata, and hence their means and standard errors are tabulated separately from the lower five strata. These relative estimates are more certain than the estimates of absolute evaporation rates. That is, runoff, leaching of water below 330 cm and variation in rainfall between observatory and forest may affect the estimate of evaporation at one site. But when we subtract the change in soil water at one site from that at an adjacent one, the average runoff, leaching and rainfall for the forest will have no effect.

Thus the index of water conservation through stomatal change, which is the change in soil water beneath untreated trees versus that beneath treated trees, can be depicted, as in Fig. 46, with confidence that we are not being misled. The Figure shows a blank for instances when the change in soil water at one of the eleven depths of observation was no less beneath treated than untreated trees. Conversely, when treatment decreased the loss, the appropriate space in the Figure is printed over more as the saving is greater.

In the first panel of the Figure, which is devoted to 1966, one can see the early savings in the two upper strata. As the upper soil dried (Fig. 37) the early, upper saving was exhausted and a saving appeared in the third, fourth and fifth strata. In 1967 and 1968 a second spray was applied, and the saving in the upper five strata grew regularly or was maintained. In 1969 with no spray but only two-thirds of the foliage remaining, a lesser saving appeared gradually. Small savings also appeared in lower strata in all years, but it is best to examine the variability of the measurements before accepting Fig. 46 as convincing evidence of a savings.

The standard error of the savings as well as the size of the savings relative to evaporation are given in Tables 22, 23, and 24. Clear evidence of a saving in evaporation and thus soil water promptly followed the first shrinkage of stomata on 3 June 1966, Table 22. In the upper six strata, where observations were numerous, the 10 mm saving was several times as large as its standard error of 2 mm. The small saving in the lower strata was insignificant. The sum of the savings, 11 mm, was 18 per cent of the total evaporation from the forest during the 2 weeks. The saving in the upper strata during the next 3 weeks was again significant. When added to an insignificant loss in the lower soil, however, the total saving was only 6 per cent of evaporation. In 1966 a second spray was not applied, new foliage overshadowed the old during July, and no further significant savings were made, but neither were the initial savings lost. Consequently, the total saving from 3 June to 4 Oc-

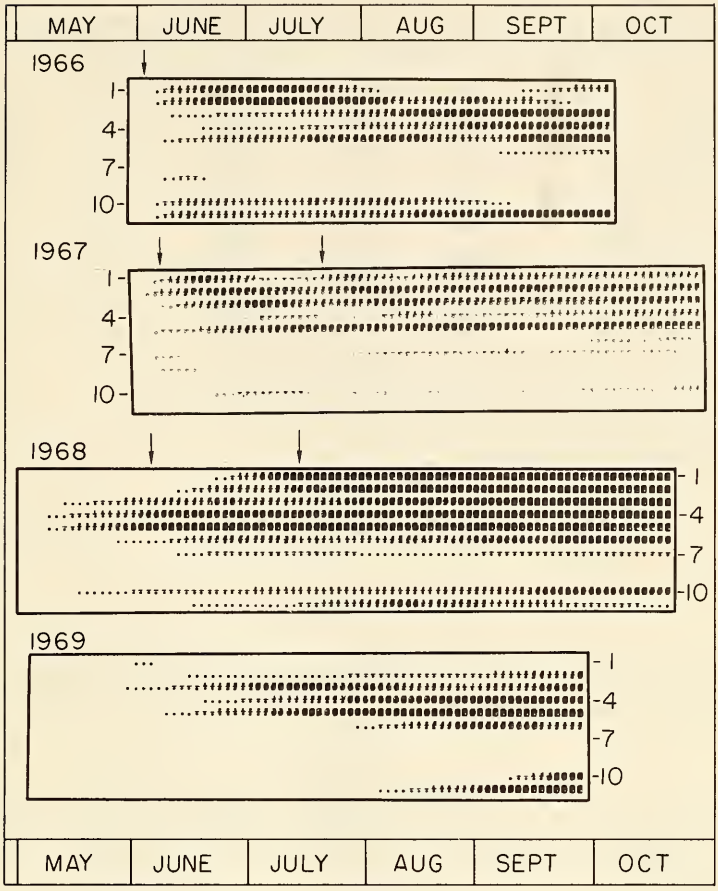

Fig. 46. The saving of water in 11 soil strata following treatment of the foliage to shrink stomata. First plantation. The arrows above the panels depicting the 4 years denote the times of spraying.

tober was significant in the upper strata, and the saving in all strata was 3 per cent of the total evaporation of the season. The failure to save more water later in the summer corresponds to the time when differences in dye infiltration through the stomata no longer differed between treated and untreated foliage (Chapter 4) and corresponds to the return of the diurnal shrinkage of the boles of the treated trees to the normal, greater shrinkage of the untreated ones (Fig. 27). It also confirmed that the earlier saving was caused by a transitory cause, the stomatal shrinkage, and not by a permanent change, such as discoloration of needles or defoliation.

In 1967 two sprays were applied, and significant savings of 13 to 25 per cent in evaporation followed, Table 23. Consequently the saving

Table 22. The water budget and saving of water by stomatal shrinkage in 1966. Standard error shown for saving.

Period	Rainfall, mm	Loss from soil, mm	Saving		
			Upper,[a] mm	Lower,[a] mm	Relative,[b] %
Jun 3 – Jun 16	37	28	10±2	1±5	18
Jun 17 – Jul 8	22	64	10±4	−5±4	6
Jul 9 – Aug 11	64	138	−7±5	1±5	....
Aug 12 – Sep 2	30	62	3±3	−3±3	....
Sep 3 – Oct 4	152	−49	5±4	0±8	....
Sum			20±7	−6±12	3
Overwinter[c]			−24±8	0±15	

[a] Upper soil is 0 to 195 cm and lower is 195 to 330 cm.
[b] Relative loss is the saving in upper and lower soil divided by the sum of rainfall and loss from soil beneath untreated trees.
[c] 4 Oct 1966 to 1 Jun 1967.

Table 23. The water budget and saving of water by stomatal shrinkage in 1967. Standard error shown for saving.

Period	Rainfall, mm	Loss from soil, mm	Saving		
			Upper,[a] mm	Lower,[a] mm	Relative,[b] %
Jun 1 – Jun 7	0	38	5±2	2±3	18
Jun 8 – Jun 14	3	50	9±1	−2±3	13
Jun 15 – Jun 28	60	−12	6±2	−1±4	10
Jun 29 – Jul 5	47	−25	1±1	−2±1	....
Jul 6 – Jul 12	6	32	0±2	3±2	8
Jul 13 – Jul 19	23	2	−3±1	−3±2	....
Jul 20 – Jul 26	9	17	5±1	1±2	25
Jul 27 – Aug 2	39	2	2±1	1±1	8
Aug 3 – Aug 10	34	3	1±1	−1±1	....
Aug 11 – Aug 16	8	15	0±1	2±1	13
Aug 17 – Aug 23	1	28	−1±1	−1±1	....
Aug 24 – Sep 6	19	57	0±1	0±2	....
Sep 7 – Sep 12	4	15	0±2	0±2	....
Sep 13 – Oct 25	135	−30	8±3	−1±4	6
Sum			34±6	−2±9	5
Overwinter[c]			−26±5	10±10	

[a] Upper soil is 0 to 195 cm and lower is 195 to 330 cm.
[b] Relative loss is the saving in upper and lower soil divided by the sum of rainfall and loss from soil beneath untreated trees.
[c] 26 Oct 1967 to 30 Apr 1968.

Table 24. The water budget and saving of water by stomatal shrinkage in 1968 and 1969. Standard error shown for saving.

Period	Rainfall, mm	Loss from soil, mm	Saving		
			Upper,[a] mm	Lower,[a] mm	Relative,[b] %
1968					
May 1 – Jun 4	118	45	13±3	−16±9	....
Jun 5 – Jun 20	32	12	14±2	6±3	46
Jun 21 – Jul 9	47	41	4±2	1±2	6
Jul 10 – Jul 15	0	32	2±1	0±1	6
Jul 16 – Aug 8	46	64	7±4	−1±4	5
Aug 9 – Oct 17	124	125	19±5	3±11	9
Sum			46±8	9±11	10
Overwinter[c]			−55±8	4±11	
1969					
May 6 – Jun 4	89	34	3±3	−7±5	....
Jun 5 – Jul 11	29	171	6±4	−1±5	2
Jul 12 – Aug 26	187	−6	14±4	1±10	8
Aug 27 – Sep 24	96	26	5±3	18±11	16
Sum			29±6	13±12	6

[a] Upper soil is 0 to 195 cm and lower is 195 to 330 cm.
[b] Relative loss is the saving in upper and lower soil divided by the sum of rainfall and loss from soil beneath untreated trees.
[c] 18 Oct 1968 to 5 May 1969.

between 1 June and 25 October was fully 32 mm or 5 per cent of the total evaporation, although no significant saving was made in the weeks well past the spraying, showing that defoliation did not cause the earlier saving.

Table 24 shows the outcome of the fewer observations of 1968 and 1969. The first spray of 1968 was followed by a significant 46 per cent decrease in evaporation, the second by a smaller saving. By the end of 1968, however, defoliation was growing substantial, and it must be considered.

An index of defoliation is provided by a summary of Table 5 and Fig. 34. The number of fascicles per cm is multiplied by the length of internode for each year's growth and added over the years. The ratios of these indices for treated versus untreated trees and for the four times of observation were: June 1968, 0.83; September 1968, 0.72; November 1968, 0.50; November 1969, 0.63. Thus, the saving in early 1968 is undoubtedly caused largely by stomatal shrinkage, but the continued saving in late 1968, even in the autumn, is undoubtedly caused by defoliation.

Since no sprays were applied in 1969, it provides us with a clear test of the effect of defoliation. The index of the preceding paragraph shows that the treated trees began the season with about half the foliage of

the untreated trees and ended the season with about two thirds. The consequence was a 6 per cent decrease in evaporation for the season. The saving in the upper soil was clearly significant. Since we calculated that a defoliation of one third would theoretically save one fifth of the evaporation, it is easy to ascribe the 6 per cent saving at the end of the experiment to defoliation.

The seemingly countless observations of soil water saving can be quickly summarized. Stomatal shrinkage, which the theoretical calculations predicted would decrease evaporation, in fact decreased evaporation by 14 mm in 1966 and 32 mm in 1967. The decreases rose near the theoretical savings rarely and only briefly after spraying, but they were statistically significant and had not disappeared by the end of the summer. Therefore, less rain was needed overwinter to return the soil beneath treated trees to field capacity, allowing 24 mm in 1966-67 and 16 mm in 1967-68 to percolate into streams and reservoirs.

The dramatic 55 mm saving of 1968 was caused by defoliation as well as stomatal shrinkage, but even then shrinkage played a role because the saving was only 42 mm in 1969 when defoliation was greater. The saving by defoliation was never observed to be more than 6 per cent.

The most important conclusion remains: by shrinking the microscopic stomata only enough to double stomatal resistance and this for only part of the season, evaporation is logically and actually substantially decreased. Thus, subtle changes in vegetation, as well as weather, can clearly have profound effects upon the hydrologic cycle.

Chapter 10

TRANSPIRATION AND ITS CONTROL—A DISCUSSION

The interconnections among many of the characters that we have observed can be depicted as in Fig. 47. Simplifying a diagram by H. Harssema and F. W. T. Penning de Vries and employing the symbols of Forrester (1969), we indicate a rate by a valve, a level by a rectangle, a controlled flow by an arrow, and information by a dotted line. Rain replenishes the level of soil water. This supplies the root and stem, which in turn hydrates the foliage. Finally, foliage loses water to the atmosphere at a rate influenced by stomata. The dashed lines for "information" merely indicate the effect, e.g. of light upon stomata, as we shall next explain in detail.

Our data from the forests demonstrate several of these connections. Let us begin at the top of the Figure. The atmosphere, either through dryness or through leaf-warming radiation, increases evaporation (Figs. 44 and 45). Stomatal closure, however, decreases evaporation (Fig. 46). Stomatal closure can be caused by PMA (Fig. 8A) or shade (Fig. 6). Closure can also be caused by a decreased level of water in the foliage

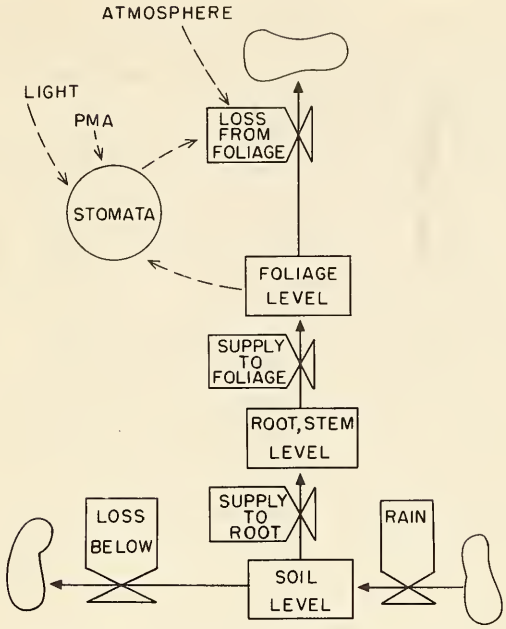

Fig. 47. A simplified scheme for the hydraulic system of a forest.

(Fig. 17), and that decreased level can follow the diurnal opening of stomata and aridity of the day (Fig. 15). On the other hand, stomatal closure by PMA allows the foliar water level to increase (Fig. 19).

By midday the loss from foliage has exceeded the supply to the roots, and the level of water in the stem is decreased as shown by contraction of its diameter (Fig. 23). This contraction, of course, lags behind the dehydration of the foliage (Fig. 25). A moister, duller day, of course, causes a smaller shrinkage of the stem than does a drier, brighter day (Figs. 21, 22 and 23). Similarly, stomata-closing PMA decreases the diurnal shrinkage of the stem (Fig. 26).

Finally, we reach the soil. The level of water in the soil is decreased at a rate depending upon the atmosphere (Figs. 44 and 45). Significantly, the loss is slower when the stomata have been closed by PMA, allowing an overwinter loss below that is added to groundwater and eventually a stream (Tables 23, 24 and 25).

Thus the small changes in stomatal resistance do, indeed, have a discernible effect upon the hydration and water movement throughout the entire plant and soil. The measured reduction in evaporation of 14 to 32 mm, although clearly discernible, is not large compared with the total annual evaporation of 600 mm. However, it did cause a similar increase in the water yield to groundwater, and thus, ultimately to the reservoirs. Moreover, in Connecticut, the amount of water lost to the atmosphere by evaporation is about equal to the amount of water that

replenishes the streams and reservoirs. In more arid regions the proportion of water lost by evaporation is greater than that which goes to groundwater, and an equivalent saving by stomatal closure could cause a more significant yield to the streams.

The 16 to 24 mm increased yield of water observed in this study is less than the 100 to 300 mm obtained in the eastern United States by the more drastic method of removing the forest (Lull and Reinhart, 1967). However, without later cutting and thinning, the increased yield of water soon disappears (Hewlett and Hibbert, 1961). Thus the relatively small savings by stomatal closure, with its advantage of leaving the forest intact, may in time prove attractive.

Before stomatal closure can be considered practical, another compound must be found, however. We emphasized at the beginning that PMA was used to establish the principle that stomatal closure would change the hydrologic cycle, even in a forest, and that PMA itself was an impractical compound. The principle has been established, and PMA remains impractical. Its impracticality derives from two characteristics. First, mercury is not suitable for widespread use. Second, in hot weather or after repeated application PMA will damage foliage and reduce growth. This damage, of course, prevents the advantageous increase in water use efficiency, which stomatal closure should cause theoretically and has caused in single leaves (e.g. Zelitch and Waggoner, 1962).

Other stomata-closing compounds have, of course, been discovered that might avoid these difficulties. Decenylsuccinic acid (Zelitch, 1964) is an example, but its closure is not consistent or persistent. In Chapter 1 we mentioned that the plant hormone, abscisic acid, has closed stomata. In an unpublished test, however, we found that pine stomata were closed 3 hours but not 4 days after spraying with abscisic acid.

Thus the search for a non-toxic compound must go on. In the meantime, however, the Voluntown experiments have shown that stomatal closure in a real stand of vegetation can decrease evaporation, promising benefits of water conservation in the soil and improved hydration in the tissue if a non-toxic stomata closer is found.

ACKNOWLEDGMENTS

The staff of the Connecticut State Park and Forest Commission at Pachaug welcomed us into their forests and buildings and helped us gladly throughout 5 years of the experiments. In 1966 Ben-Ami Bravdo, now at the Hebrew University, Rehovot, helped mightily to start the experiments. In 1967 R. C. Ellis made the extensive observations of soil water and the dendrometers. J. E. Begg, G. R. Carlson, D. B. Downs, D. E. Hill, Mrs. B. Kennedy, and P. F. Tomlinson also made valuable contributions. This study was supported, in part, by the McIntire–Stennis Fund.

LITERATURE CITED

Baumgartner, A. 1965. The heat, water and carbon dioxide budget of plant cover: methods and measurements, p. 495-512. *In* Methodology of Plant Eco-Physiology. Proc. of the Montpelier Symposium. UNESCO, Paris.

Baumgartner, A. 1967. Energetic bases for differential vaporization from forest and agricultural lands, p. 381-389. *In* W. E. Sopper & H. W. Lull (eds.), Forest Hydrology. Pergamon Press, Oxford.

Bormann, F. H. and T. T. Kozlowski. 1962. Measurements of tree ring growth with dial-gage dendrometers and vernier tree ring bands. Ecology 43:289-294.

Boyer, J. S. 1967. Leaf water potentials measured with a pressure chamber. Plant Physiol. 42:133-137.

Brown, K. W. and W. Covey. 1966. The energy-budget evaluation of the micrometeorological transfer processes within a cornfield. Agr. Meteorol. 3:73-96.

Daubenmire, R. F. 1945. An improved precision dendrometer. Ecology 26:97-98.

Davenport, D. C. 1967. Effects of chemical antitranspirants on transpiration and growth of grass. J. Exp. Botany 18:332-347.

De Roo, H. C. 1969. Leaf water potentials of sorghum and corn, estimated with the pressure bomb. Agron. J. 61:969-970.

De Roo, H. C. 1970. Leaf water potentials of tobacco, estimated with the pressure bomb. Tob. Sci. 14:105-106.

Forrester, J. W. 1969. Urban Dynamics. M.I.T. Press, Cambridge, Mass. p. 13.

Fritts, H. C. and E. C. Fritts. 1955. A new dendrograph for recording radial changes of a tree. Forest Sci. 1:271-276.

Fry, K. E. and R. B. Walker. 1967. A pressure-infiltration method for estimating stomatal opening in conifers. Ecology 48:155-157.

Haasis, F. W. 1934. Diametral changes in tree trunks. Carnegie Inst. Wash. Pub. 450. 103 p.

Hewlett, J. D. and A. R. Hibbert. 1961. Increases in water yield after several types of forest cutting. International Ass. Sci. Hydrol. 6:5-17.

Hewlett, J. D., J. E. Douglass and J. L. Clutter. 1964. Instrumental and soil moisture variance using neutron scattering method. Soil Sci. 97:19-24.

Hill, D. E. 1959. The storage of moisture in Connecticut soils. Conn. Agr. Exp. Station. Bull. 627. 30 p.

Hunter, A. S. and O. J. Kelley. 1946. A new technique for studying the absorption of moisture and nutrients from soil by plant roots. Soil Sci. 62:441-450.

Jones, R. J. and T. A. Mansfield. 1970. Suppression of stomatal opening in leaves treated with abscisic acid. J. Exp. Botany 21:714-719.

Kaufmann, M. R. 1968a. Evaluation of the pressure chamber technique for estimating plant water potential of forest tree species. Forest Sci. 14:369-374.

Kaufmann, M. R. 1968b. Evaluation of the pressure chamber method for measurement of water stress in citrus. Proc. Amer. Soc. Hort. Sci. 93:186-190.

Keller, T. 1966. Über den Einfluss von Transpirationshemmenden Chemikalien (Antitranspirantien) auf Transpiration, CO_2—Aufnahme und Wurzelwachstum von Jungfichten. Forstwiss. Centr. 85:65-79.

Kienholz, R. 1934. Leader, needle, cambial and root growth in certain conifers and their interrelations. Bot. Gazette 96:73-92.

Klemmer, L. 1969. Die Periodik des Radialzuwachses in einem Fichtenwald und deren meteorologische Steuerung. Universität München, Meteorologisches Institut, Wissenschaft iche Mitteilungen Nr 17. 85 p.

Kramer, P. J. 1969. Plant and Soil Water Relationships: A Modern Synthesis. McGraw-Hill, New York. p. 320-322.

Larson, P. R. 1964. Contribution of different-aged needles to growth and wood formation of young red pines. Forest Sci. 10:224-238.

Loftfield, J. V. G. 1921. The Behaviour of Stomata. Carnegie Inst. Wash. 104 p.

Lull, H. W. and K. G. Reinhart. 1967. Increasing water yield in the Northeast by management of forested watersheds. U.S. Forest Service Research Paper. NE-66. 45 p.

MacDougal, D. T. 1921. Growth in trees. Carnegie Inst. Wash. Pub. 307. 41 p.
Mittelheuser, C. J. and R. F. M. Van Steveninck. 1969. Stomatal closure and inhibition of transpiration by RS-abscisic acid. Nature 221:281-282.
Monteith, J. L. and T. A. Bull. 1970. A diffusive resistance porometer for field use. II. Theory, calibration and performance. J. Appl. Ecol. 7:623-638.
Oppenheimer, H. R. and N. Engelberg. 1965. Mesure du degré d'ouverture des stomates de conifères méthodes anciennes et modernes, p. 317-323. *In* Methodology of Plant Eco-Physiology. Proc. of the Montpelier Symposium. UNESCO, Paris.
Penman, H. L. 1956. Evaporation—an introductory survey. Neth. J. Agr. Sci. 4:9-29.
Penman, H. L. 1967. Evaporation from forests: a comparison of theory and observation, p. 373-380. *In* W. E. Sopper and H. W. Lull (eds.), Forest Hydrology. Pergamon Press, Oxford.
Reineke, L. M. 1932. A precision dendrometer. J. Forestry 30:692-699.
Rutter, A. J. and D. F. Fourt. 1965. Studies in the water relations of *Pinus sylvestris* in plantation conditions. III. A comparison of soil water changes and estimates of total evaporation on four afforested sites and one grass-covered site. J. Appl. Ecol. 2:197-209.
Saeki, T. 1963. Light relations in plant communities, p. 79-94. *In* L. T. Evans (ed.), Environmental control of plant growth. Academic Press, N.Y.
Sampson, J. 1961. A method of replicating dry or moist surfaces for examination by light microscopy. Nature 191:932-933.
Scholander, P. F., H. T. Hammel, E. D. Bradstreet and E. A. Hemmingsen. 1965. Sap pressure in vascular plants. Science 148:339-346.
Scholander, P. F., H. T. Hammel, E. A. Hemmingsen and E. D. Bradstreet. 1964. Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. Proc. Nat. Acad. Sci. U.S. 52:119-125.
Shaw, R. H. 1956. A comparison of solar radiation and net radiation. Bull. Amer. Meteorol. Soc. 37:205-206.
Shimshi, D. 1963a. Effect of chemical closure of stomata on transpiration in varied soil and atmospheric environments. Plant Physiol. 38:709-712.
Shimshi, D. 1963b. Effect of soil moisture and phenylmercuric acetate upon stomatal aperture, transpiration and photosynthesis. Plant Physiol. 38:713-721.
Slatyer, R. O. and J. F. Bierhuizen. 1964. The effect of several foliar sprays on transpiration and water use efficiency of cotton plants. Agr. Meteorol. 1:42-53.
Stålfelt, M. G. 1962. The effect of temperature on opening of the stomatal cells. Physiol. Plant. 15:772-779.
Stephens, G. 1969. Productivity of red pine. 1. Foliage distribution in tree crown and stand canopy. Agr. Meteorol. 6:275-282.
Tadaki, Y. 1966. Some discussions on the leaf biomass of forest stands and trees. Government For. Exp. Sta., Tokyo. Bull. 184, p. 135-161.
Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Geogr. Rev. 38:55-94.
Turner, N. C. 1969. Stomatal response to illumination in three contrasting canopies. Crop Sci. 9:303-307.
Turner, N. C. and L. D. Incoll. 1971. The vertical distribution of photosynthesis in crops of tobacco and sorghum. J. Appl. Ecol. 8: (In press).
Turner, N. C. and J.-Y. Parlange. 1970. Analysis of operation and calibration of a ventilated diffusion porometer. Plant Physiol. 46:175-177.
Turner, N. C. and P. E. Waggoner. 1968. Effects of changing stomatal width in a red pine forest on soil water content, leaf water potential, bole diameter, and growth. Plant Physiol. 43:973-978.
Turner, N. C., H. C. De Roo and W. H. Wright. 1971. A pressure chamber for the measurement of plant water potential. Conn. Agr. Exp. Sta. Special Soils Bull. 33, 9 p.
Turner, N. C., F. C. C. Pedersen and W. H. Wright. 1969. An aspirated diffusion porometer for field use. Conn. Agr. Exp. Sta. Special Soils Bull. 29, 12 p.

Uchijima, Z. 1962. Studies on the microclimate within plant communities. I. On the turbulent transfer coefficient within plant layers. J. Agr. Meteorol., Tokyo, 18:1-19.

U.S. Bureau of the Census. 1970. Statistical Abstract of the United States. 91st edition. U.S. Government Printing Office. Washington, D.C. p. 171.

U.S. Department of Agriculture. 1951. Soil Survey Manual. U.S. Dept. Agr. Handbook 18. U.S. Government Printing Office. Washington, D.C. 503 p.

Van Bavel, C. H. M., D. R. Nielson and J. M. Davidson. 1961. Calibration and characteristics of two neutron moisture probes. Soil Sci. Soc. Amer. Proc., 25:329-334.

Ventura, M. M. 1954. Ação de inibidónes enzimãticos sôbre a transpiraçâo e o comportamento dos estômatos. II. Ação do Arsenito, 2,4-dinitrofenol e verde de Janus sôbre fôlhas isolades de *Stizolobium aterrimum*. Pip. o Trac. Rev. Brasil Biol. 14:153-161.

Wadsworth, D. F. 1960. Chemical control of disease affecting turf on golf greens. Golf Course Reporter 28(3):26-30.

Waggoner, P. E. 1967. Transpiration of trees and chemicals that close stomata, p. 483-489. *In* W. E. Sopper and H. W. Lull (eds.), Forest Hydrology. Pergamon Press, Oxford.

Waggoner, P. E. and B. Bravdo. 1967. Stomata and the hydrologic cycle. Proc. Nat. Acad. Sci. U.S. 57:1096-1102.

Waggoner, P. E. and J. D. Hewlett. 1965. Test of a transpiration inhibitor on a forested watershed. Water Resources Res. 1:391-396.

Waggoner, P. E. and W. E. Reifsnyder. 1968. Simulation of the temperature, humidity and evaporation profiles in a leaf canopy. J. Appl. Meteorol. 7:400-409.

Waggoner, P. E., J. E. Begg and N. C. Turner. 1969a. Evaporation of dew. Agr. Meteorol. 6:227-230.

Waggoner, P. E., G. E. Furnival and W. E. Reifsnyder. 1969b. Simulation of the microclimate in a forest. Forest Sci. 15:37-45.

Waggoner, P. E., J. L. Monteith and G. Szeicz. 1964. Decreasing transpiration of field plants by chemical closure of stomata. Nature 201:97-98.

Wallihan, E. F. 1964. Modification and use of an electric hygrometer for estimating relative stomatal aperture. Plant Physiol. 39:86-90.

Waring, R. H. and B. D. Cleary. 1967. Plant moisture stress: evaluation by pressure bomb. Science 155:1248-1254.

Worrall, J. 1966. A method of correcting dendrometer measures of tree diameter for variation induced by moisture stress changes. Forest Sci. 12:427-429.

Zelitch, I. 1961. Biochemical control of stomatal opening in leaves. Proc. Nat. Acad. Sci. U.S. 47:1423-1433.

Zelitch, I. 1964. Reduction of transpiration of leaves through stomatal closure induced by alkenylsuccinic acids. Science 143:692-693.

Zelitch, I. and P. E. Waggoner. 1962. Effect of chemical control of stomata on transpiration and photosynthesis. Proc. Nat. Acad. Sci. U.S. 48:1101-1108 and 1297-1299.

THE CONNECTICUT
AGRICULTURAL EXPERIMENT STATION
NEW HAVEN, CONNECTICUT 06504
James G. Horsfall
Director

PUBLICATION

POSTAGE PAID
United States Department of Agriculture

University of
Connecticut
Libraries

39153029115146